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I. THE NATURE OF PHYSIOLOGICAL RESPONSE

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LIVING plants could hardly have been observed at all without recognition of the fact that they are affected by external conditions. These effects, when first observed, were undoubtedly interpreted as mere conditions of living, and our interpretation to-day has hardly gone beyond this. A moderate temperature, an adequate supply of water, and the normal light are necessary for green plants; and when these conditions are suitable the general behavior of the plant is affected. All its processes have a healthy *tone;* it flourishes; and the factors which operate to produce this condition are declared to be *tonic.*

When the effects of external agents are studied more closely, several peculiarities appear. Even these tonic factors are seen frequently to produce quite limited changes in behavior, though they may act simultaneously upon all parts of the body. Especially is this the case when there is some sudden change in the intensity or direction of these factors. Thus if the air temperature falls a few degrees on some spring day when the crocuses are in bloom, the perianth segments promptly curve inwards and close the flower. Or if the sunlight is

[1] Invitation papers read at the sixteenth annual meeting of the Botanical Society of America, Boston, 1909.

obscured by clouds, the dandelion heads are soon folded together by the straightening up of the involucral bracts. No other changes are visible, though others may be detected by appropriate means.

Again, external agents may act on only a limited region of the plant, in which case the obvious effects may be restricted to some special part, either that immediately acted upon or one at a greater or less distance from it. Thus if the cotyledon alone of a *Panicum* seedling be lighted from one side, the hypocotyl, 20 mm. or more away, instead of continuing its equal growth, may curve abruptly.

In these two cases of limited visible change, the phenomena are explained by asserting that the protoplasm is *irritable* and *responds* to an external change called a *stimulus*. In fact, there is an inclination, after endowing the protoplasm with such "properties" as "irritability," "automaticity" and "self-regulation," to be satisfied with the words and there make an end. Such a tendency, wide-spread in the prescientific days, undoubtedly springs from the wonder with which one confronts an uncomprehended intricate mechanism. It finds expression, for example, in a common saying about this or that industrial machine: "It seems to have almost human intelligence." Of course no one supposes the machine really endowed with other than physical qualities, operating through the matter and the energy with which it is supplied. Yet the vitalism, which dominated the earlier years of physiology, even yet controls our speech and our thinking, and indeed lately shows signs of revival.

Vitalism, assuming living matter to be endowed with special powers, called vital in distinction from physical, is itself in part an expression of helplessness in the face of an uncomprehended mechanism, the living body, and in part an interpretation of nature in terms of our own consciousness. To seek explanation in that direction is to proceed from the simple to the complex; but the explanation of phenomena must be a process of analysis,

not of synthesis, and so of necessity proceeds in the other direction. We may not believe it possible to account for the behavior of living things by considering them as mechanisms whose actions are to be described in terms of matter and energy; and certainly it is not possible to do this now for any but the simplest actions. Yet it must not be forgotten that all the progress that has been made has been made in this direction; so that it commends itself to us both by the *a priori* and the inductive method.

The phenomena of response are probably the most complicated to be seen in the plant, and as yet we are far from being able to describe them completely in terms of physics and chemistry. I purpose only to present some suggestions on the nature of these phenomena, as a contribution toward the mechanistic conception of the plant, in the hope that this presentation may help to rid us of some of the subconscious vitalistic notions that are apt to cling so persistently about our thought and speech.

First let us consider the relation of the phenomena of response in living and non-living matter. To speak of response by non-living matter can occasion no surprise. Sachs, long ago, in his "Lectures on the Physiology of Plants," pointed out the fact that response is not peculiar to living things, citing as an example the crystals of the yellow iodide of mercury, which change their constitution and color when stimulated by various agents—a scratch sufficing to initiate a change which spreads gradually through the whole. Many other substances behave similarly. To explain such a change we predicate a state of metastable molecular equilibrium, the upsetting of which at one point incites a spreading disturbance, as a row of properly spaced blocks fall.

There is another sort of response in non-living matter, which is conditioned by external factors. In moist air many anhydrous salts and oxids unite with water, and in some cases in proportions differing with the amount of the vapor pressure. Thus, anhydrous copper sulfate, at a temperature of 50° C. with the vapor pressure gradually increasing from zero, would take up one molecule of

water and become the monohydrate as soon as the vapor pressure reached 4.5 mm. of mercury. As soon as it reaches 30 mm. the monohydrate takes up two more molecules and becomes the trihydrate; while at 47 mm. and above the trihydrate adds two more molecules and becomes the pentahydrate. Conversely, should the vapor pressure fall below 47 mm., the pentahydrate loses water and is transformed into the trihydrate, and so on. The constitution of the copper sulfate, in fact, precisely responds to the vapor pressure of water around it. Many like cases might be cited. The peculiarity of these is that while the external factor may change steadily, the physical response will be discontinuous. Among the multifarious phenomena of irritability in plants are some which are so nearly parallel to the behavior just described as to suggest an analogous causation.

It is possible that the application of the term irritability to the behavior of crystals will seem an unwise straining of its usual sense. Irritability has often been enumerated among the distinguishing properties of protoplasm. Even Sachs wrote:

> Irritability is the great distinguishing characteristic of living organisms; the dead organism is dead simply because it has lost its irritability.

But if we are to consider irritability as a property—a characteristic—of protoplasm, it must be understood to be a conditional property, as strictly limited by circumstances as are the properties of non-living matter. Steel may be highly tenacious at certain temperatures; but at the temperature of liquid air it is as brittle as glass and can be pulverized by a blow. A frond of *Laminaria* when wet is a tough flexible strap, but when dry it is so rigid and brittle that it can be broken to fragments by slight bending. Many a plant is clearly irritable at moderate temperatures when well watered and lighted, but loses its irritability completely under adverse conditions. Becquerel has dried seeds for six months in a vacuum with barium hydroxid at 40°, sealed them for a year in a glass tube exhausted to 0.002 mm. of mer-

cury, kept them in liquid air at a temperature of — 190° for three weeks and in liquid hydrogen (— 250°) for three days. Is it possible to conceive of irritability existing under such conditions? Is it, indeed, possible to conceive of life as latent? I think not. Irritability must be counted as completely lost during this time, and as regained when the seeds germinated, as they did when suitable conditions were furnished. To emphasize the conditional nature of this quality, it may be better to describe protoplasm when irritable as in a state or condition, instead of following the example of the physicist in saying that it possesses the property of irritability, of which it may be as surely dispossessed as steel may be of its tenacity.

Of recent years Bose has the merit of having insisted upon the essential similarity of response in living and in non-living matter. His "Plant Response" and "Comparative Electro-physiology" are based upon this conception; and though they contain much that can not be approved, I am in complete accord with the thesis that plants are intelligible only as mechanisms whose behavior, though more complicated than that of non-living systems, is to be described by analogous laws.

While recognizing the essential unity manifest in the behavior of all matter, we must nevertheless discriminate between physical and physiological response. It is not possible, however, to use these terms as they have been used, even by Bose, to designate, respectively, the response of non-living and living matter, since many of the responses of organisms are purely physical. Physical response, as I conceive it, is marked by the fact that the energy applied to the body is a full measure of the effect produced. Thus, when the conductivity of a selenium plate is altered by light, the molecular disturbance (if we so explain it) is initiated by the radiant energy, and the effect is precisely measured by the energy applied from the outside. The selenium contributes nothing. It is acted upon, and its condition is altered for the time

being, by the external agent. The effect dies out shortly after the agent ceases to act. Whether there is a loss of energy or a gain, no further change ensues in the system, unless it is acted upon from the outside.

Physiological response, on the other hand, though at bottom of the same sort, differs in that the external agent produces an upset that releases energy previously accumulated, so that the effect exceeds that due to the initial energy acting upon the organism. That is why, indeed, the term *stimulus* was originally applied to such an agent; it brings into action energy often vastly greater than its own. In this case there is a run-down of energy. The system contains less than before by as much work as has been done in response to the stimulus. Repeated responses lead to exhaustion of the accumulated energy, when further stimulation is impotent. To explain such a situation Bose's theory of molecular strain is inadequate; we are driven to take account of stored energy, and not a direct supply. For if the depleted system be kept under conditions as nearly uniform as possible, it proceeds to recover energy by the incorporation of new material with its potential energy. The protoplast assimilates food and presently is ready for new response to any stimulus. It is the cyclic character of their energetics that characterizes living things, no less in the phenomena of response than in nutrition.

Even a casual examination of the various responses of an organism shows clearly that some of them are to be classed with the physical and others with the physiological, as above defined. If so, it is plain that it is not mere responsiveness that marks living things, for non-living matter responds; it is the ability after a loss of energy by response to regain, by the aid of the environment, a condition which makes response possible once more. This is no mere restoration of a molecular equilibrium which has been disturbed or relief from molecular strain; it involves acquisition of energy. How far this is due to a direct intake of energy and how far to the utilization of potential energy in available foods, our present knowl-

edge of the energetics of plants does not enable us to decide. Certainly we can not accept the source proposed by Bose, when he writes:

> And now we see that the fine ramifications of fibrovascular elements over as wide an area as possible in the leaf provides a virtual catchment basin for the reception of stimulus. The expanded lamina is thus not merely a specialized structure for the purpose of photosynthesis, but also a sensitive area for the absorption of stimulus, the effect of which is gathered into larger and larger nerve trunks in the course of its transmission downwards into the body of the plant.

It is of course possible to use the term *stimulus* to designate any external or internal agent that produces an effect upon the organism, and *response* for the effect produced; but that use of the terms tends to confusion. Yet, besides the erratic treatises of Bose, some recent text-books use the words in this way. One, for example, reads: "Responses to water stimuli.—The primary responses of the plant to the water of the habitat are four: namely, absorption, diffusion, transport, and transpiration." It is hardly necessary to point out that if such processes are responses, then every change that occurs in nature is a response and every agent a stimulus. By such a usage we should lose the whole value of the discrimination embodied in the terms.

The less clearly plant processes are conditioned by the environment, the more likely they are to be reckoned responses to stimuli. Growth, for example, is often considered a response to stimuli; but it seems most likely that it is quantitatively determined by various factors (turgor, temperature, oxygen, food, etc.), any one of which may limit it. Stimulation by gravity or light may be an added factor, interlocking with one or more of them, and, by inducing local variation in the rate of growth, producing curvature; which is obviously a physiological response, for when the effect of the stimulus passes away the ordinary rate may be resumed.

In considering the energetics of response, it is essential not to forget that many stimuli *inhibit* actions going on at the time excitation occurs. There are many familiar examples of this among animals, but few in plants.

One well known is the interference of stimuli in tendrils. As Fitting showed, friction on the dorsal side of tendrils which usually curve after irritation of the ventral side, inhibits the curvature, not by setting up a countervailing rate of growth, for it apparently has no power to influence growth, but by interfering with the reaction somewhere between perception and the growth response. Here, if the stimulus were a source of energy, or limited the reaction, the double excitation should produce a doubly strong response. Nor can the well-known interference of light or sound waves in unlike phases be cited as an analogy of the inhibition in this case, because no such superposition is possible. It must be admitted that in cases of this kind the energy of the stimulus is not directly related to the response.

Of course, in urging this I must not be understood as denying that the excitation is often proportional to the intensity and duration of the stimulus, and that the final response may be influenced by the amount of excitation; the point is only that potential energy is released in amounts not at present referable quantitatively to that of the stimulus.

On analyzing the varied reactions to stimuli, it will be found in many cases that it is possible to recognize two well-marked phases, which may be designated *primary* and *secondary*. In other cases no such distinction can be made. One of the primary phases of response is known as *perception*, a word which, as used by plant physiologists, is entirely without psychological implications. Whatever change in the protoplasm is connoted by that term takes place almost instantly, as shown by the phenomena of summation. Stimuli of extremely brief duration—say a small fraction of a second—so transient that they produce no observable effect, nevertheless, if repeated at proper intervals, finally give rise to a reaction. The brevity of each period of stimulation gives indication of the speed of the perception change; for if no effect were produced by a single stimulus, repetition could have no effect.

Another primary phase of response is the propagation of the excitation. The disturbance called perception propagates itself, that is, it initiates in adjacent material a corresponding change, progressing from point to point, as shown by secondary effects produced at a greater or less distance from the point where the stimulus is applied. The precise character of the change itself has been little studied in plants, though the rate of propagation is known to be of the same order of magnitude as that in the nerves of the lower animals—say 1 to 10 mm. per second.

The secondary phase of response is manifested either separately by turgor mechanisms and by growth mechanisms, or by the two conjointly. In turgor mechanisms altered turgor of the cells in a definite region causes displacement of parts attached. In growth mechanisms local differences in the rate of growth of the organ displaces the adjacent parts. When combined the earliest displacement is due to turgor, and this is made permanent by growth.

Examples are so familiar that they need hardly be cited, and a single one of each will suffice. When the tip of a leaflet of *Mimosa* is stimulated by burning with a lens, the excitation is propagated to the petiolule of the leaflet, the turgor of its upper and anterior cells is so reduced that those on the opposite side compress them, bending the petiolule sharply and so carrying the leaflet forward and upward. The disturbance may spread to other leaflets and even to the base of the petiole, with appropriate curvatures in each motor organ.

When a primary root is placed horizontal, perception occurs mainly in the tip, the excitation is propagated backward, and the secondary response appears as differential growth of the cells chiefly in the third and fourth millimeter from the tip, which produces the well-known curvature.

Though much discussed, it is not clear whether the secondary response of tendrils depends on a growth mechanism or a turgor mechanism. I am inclined to be-

lieve that there is here a combination, the first curvature being due to a turgor change, which is fixed with unusual promptness by growth.

The movements of minute motile organisms, whether autonomous or induced, can hardly be analyzed, so intimate are the relations of the primary and secondary phases of response, if indeed they are separable.

All physiological responses when analyzed show the same general relations, no matter how varied the stimuli and the end reactions. If there were nothing more than the general applicability of Weber's law, this would be enough to suggest that there is some fundamental unity in the responses. There are, however, many other features that point in the same direction. It is obvious that the common factor is not to be found in the later phases of the response, where the structure of the organ may play a determinative rôle; nor in the direction from which the stimulus acts, which is known to determine often the direction of movement. Bose has sought to show that all cells when stimulated exhibit two concomitant responses, by which, it seems, he would account for all the phenomena of plant life, even to the ascent of water! Without assenting to his applications of the observations, we must say that Bose has done good service in showing that a mechanical contraction follows stimulation, and that change in electric potential occurs simultaneously. This, I think, we may consider established for a large number of plants, and it is very likely true of all. A study of the negative electric variation leaves us quite in the dark as to its significance, and though we are constantly tempted by electric analogies in the description of nervous phenomena, we gain no real insight yet into the rôle of electric stresses in organisms, because our knowledge of their causation is too vague.

In concomitant contraction and electric variation we have a two-phase phenomenon, which should be capable of further analysis. Is there any simpler action—more fundamental—which may produce both? To this question the recent work of Lepeschkin and Tröndle, supple-

menting earlier investigations, suggests an answer. Turgor variations have long been studied, but a reason for them has been sought in vain. We now know that various agents change the permeability of the protoplast to solutes, and that this sensitiveness is not limited to the specialized cells of a gland or a motor organ, but characterizes even the mesophyll. That this behavior occurs where there is no obvious relation to the functions of the organ, suggests at once that it inheres in the protoplast as a fundamental quality, in virtue of its chemical constitution or its molecular structure. It is perfectly easy to understand that this structure may be modified by the radiant energy already known to alter the permeability of the protoplast; and many other stimuli are of a kind to influence the unstable chemical compounds that compose protoplasm. If that estimate be verified by further researches, we shall be justified in considering *variability in permeability* as a basic property of protoplasts.

It will be evident enough that a change in permeability will permit the escape of some of the cell sap, with consequent shrinkage of the protoplast, stretched as it is by osmotic pressure, so that Bose's contraction would naturally result. Whether the escape of the solutes would account for the negative electric variation, I do not pretend to say, for the present theories as to electromotive force do not afford any light on the situation. Therefore, until the relation of electric stresses to other phenomena is better known, we must leave this question in abeyance.

The primary and secondary phases of a response may be understood readily in conformity to this conception. The sufficient stimulus or the summated excitation changes the constitution of the protoplast, and this change spreads along the protoplasmic lines of communication, until it reaches a region where the changed turgor results in a curvature, either directly, as in turgor mechanisms, or indirectly, by altering the rate of growth, as in growth mechanisms. That the turgor changes reported in the root undergoing geotropic curvature apparently do not harmonize with this theory is probably due

to the untimeliness of the observations. It is said that when the curvature is taking place the turgor of the cells on the concave side is unchanged and on the convex side lowered. But by the time curvature is well under way, the turgor conditions immediately following excitation may have undergone complete alteration, if we may judge from similar changes in motor organs. Thus, the original turgor, lowered on excitation (according to theory) by the increased permeability of the under side, may have been regained, while the very growth itself of the convex side may be responsible for the reduced turgor then observed on that side.

The responses of recoil and orientation in motile organisms are easily interpretable in terms of this conception, and though the application is purely hypothetical, it is no more so than the current explanations. Just such a change as results in changed permeability of the walled protoplast to solutes of the great vacuoles might take place on the passage of a naked protoplast into or out of a stimulation zone. How such a change can reverse the mechanism of movement is not explicable at present; but the new conception introduces no new difficulty. For example: If a change in surface tension is predicated as the result of excitation and the occasion of recoil, it is just through some change in chemical constitution that such an alteration in surface tension might come about. If the organism be one which orients itself to one-sided stimuli, orientation may as easily result from a local change in constitution as in any of the ways assumed by current theory.

No one is more keenly aware than I that these all are matters of speculation. They are presented as such. My hope is that they will direct attention to this phase of plant behavior and will stimulate thought, which should first clarify our conceptions, and then suggest lines of research.

II. THE PLACE OF PLANT RESPONSES IN THE CATEGORIES OF SENSITIVE REACTIONS

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MORE than two decades ago in the hands of Darwin, Sachs, Wiesner, Pfeffer, Strasburger, Stahl and others, the principal sensitive reactions for both fixed and free-moving plants had been determined. At that period, in animal biology only a few scattered papers had appeared on sensitive reactions. The zoologists approached this study through human psychology; starting with intelligence and reflexes in the highest animals, they cast a glance now and then toward the lower metazoa, and talked of reflexes and instinct. Plants, not standing in the line of descent which has its climax in man, were studied in an objective manner with no attempt to bring their reactions into a scheme of comparative psychology.

For the past two decades more attention has been paid to the study of behavior in the lowest animals, with the result that a great body of literature has already arisen, some of it tainted with anthropomorphism, but the most of it describing simply and carefully the reactions of the protozoa and the lower metazoa.

This independent activity on the part of the plant and animal biologists has resulted in the upbuilding of two almost independent bodies of literature on the behavior of lower organisms. Such early workers in the field as Verworn and Loeb compared and identified the reactions which they saw in the lower animals with those already published for plants; but as the zoologists have worked on, and more workers have come into the field, there has arisen among the botanists a feeling of uncertainty as to the significance of the terminology employed by the zoologists, and a hesitation in identifying plant reactions with those of the lowest animals. Thus, Francis

Darwin, in his presidential address before the British Association for the Advancement of Science in 1908,[1] intimates that he does not understand Loeb's use of the term "tropism." Botanists, probably quite generally, are in doubt as to whether Jennings's "trial and error" description can be applied to plant reactions. The existence of these two bodies of literature, and the uncertainty as to the significance of terms, calls, to my mind, for an examination of the phenomena of response in plants and in the lower animals, to the end that doubt may be removed as to the applicability of the same terms to both plant and animal response.

Proceeding to compare these two groups of organisms, we may say that both have fixed and free-moving forms. Most of the plants are fixed, and a group of their well-known reactions which botanists call "tropisms" are exactly simulated on the animal side by hydroids, as recorded by Loeb.[2] Geotropic and heliotropic bendings of the so-called stems and the so-called roots of the hydroids differ in no way from the manifestations of these phenomena in the stems and roots of plants.

Most of the lower animals are free-moving, and it is upon the phenomena of movement in these forms that the most of the animal studies have been made. Among plants, corresponding studies have been made upon the movements of bacteria, antherozoids and the swarm-cells of algæ and fungi. A study of the literature describing the behavior of the protozoa and of the free-moving plants must convince one that the stimuli and the responses are the same in both divisions of organisms. There are animals with amœboid movements and plants with amœboid movements, both animals and plants with cilia, and both with flagella. We may go a step farther, and consider the stimuli that influence the movements of these plants and animals. We have learned that both are directed in their behavior by gravitation, light, chemicals and the electric current. The behavior in the plant

[1] *Science*, XXVIII, 353.

[2] "General Physiology," I, 103.

group can be described by the same terms as used for the animal group.

Before proceeding farther in the comparison of plant and animal responses, we must consider the relation of responses in fixed forms to those in free-moving forms. It is well known that botanists generally use the terms "tropism" and "taxis" to distinguish movement in the fixed organisms from that in the free-moving. Some zoologists also, among them Verworn, observe the same practise. The majority of zoologists, however, following the lead of Loeb, omit the "taxis" designation wholly, and include the movements of both fixed and free-moving forms in the term "tropism." This is merely a question of terminology, and need not occupy our time here. It is more important to consider whether the behavior of the fixed and that of the free-moving lower organisms are enough alike to be regarded as fundamentally the same. We may cite an analogy by saying that a traction engine may one hour be pulling a load along a road, and the next hour it may be stationary and operating a threshing machine. To enable it to do the one or the other requires but a slight alteration in the form of connection of its parts, a slight change in its mechanism. A swarm cell of the alga, *Ulothrix,* may alter its direction under the application of a slight stimulus, and swim toward the source of light. It may, a short time later, fix itself to the substratum, and now bend as a fixed organism toward the source of light. One can readily believe that the two reactions are the same except for the difference in the mechanism.

Besides the evidence for the fundamental similarity of sensitive processes in fixed and free-moving organisms furnished by the foregoing example, is the evidence presented by the quality of relation of stimulus and response in the two kinds of organisms: Both kinds of organisms, according to their structure, show simple positive or negative movements toward or away from the source of stimulation; both kinds are sensitive to the same kinds of

stimuli, such as gravitation, light and chemicals; and both kinds vary their response according to their *physiological state.* In the various published observations which treat of the reactions of fixed and free-moving organisms, the authors regard the responses as belonging to the same class; and we may so regard them here. It might be said also, that the majority of reactions in the middle and higher metazoa are regarded by some as the same in kind, differing only in degree from the reactions of the protozoa. With the more complex reactions of the higher metazoa, botanists have little to do.

What now are the characteristics of these sensitive phenomena in plants and animals by which we class such phenomena together?

1. On both the plant and the protozoan side, the organisms possess no nerve cells. We used to be taught that for a reflex action there must be an afferent nerve, a ganglion and an efferent nerve. Such a chain is no longer necessary for a reflex according to definition. Pfeffer speaks of reflex acts in plants, and Massart, Jennings, Bohn and others expressly state that the tropisms of plants and nerveless animals are to be denominated reflexes, or, more specifically, *non-nervous reflexes.*

2. By the term "tropisms" (including "taxims"), the botanist has understood those direction movements of plants due to external stimuli, such as gravitation, light and chemicals. But this use of the term is now too broad.

The zoologists apply the same term to similar movements of the lower animals. But not all zoologists adopt the definition of a tropism as the definition is understood by the botanists. To the botanist, "tropism" always implies a response due to what is known as the *indirect* action of a stimulus; that is, the stimulus produces first an excitation, the excitation sets up a wave, or impulse, which is transmitted to the reaction protoplasm, whose action gives the sensitive response. The controversy

over the implied meaning of "tropism" as applied to animals seems to have arisen mostly through the attempts of Loeb and his followers to simplify the conception of the sensitive processes, to conceive of the stimulus as *directly* producing the reaction, as one might think of a heliotropic curve in a marine annelid produced directly by the sun's rays shortening the muscles on the sunward side. The controversy among the zoologists wages about the terms *direct* and *indirect*. Indeed, the banners of the opposing forces may be said to bear respectively but these two mottoes. On the one side the herald has proclaimed these terms to the satisfaction of the botanists; that is, all sensitive reactions are *indirect;* that is, they are complex, the stimulus producing a change in the protoplasm, local or wide-spread, and this excitation of protoplasm producing an impulse, over a lesser or greater distance, setting in operation, or releasing, energy which brings the visible response. On the other side, the terms are but obscurely defined, and the nearest we come to a definition is that the excitation and the reaction are local.

Among plants there may be cases in which the excitation and reaction are local, and there are certainly cases in which a considerable part of the plant is affected. Rothert, experimenting with the coleoptile of the oat, found that he could induce positive heliotropism when only the basal, motile, part was illuminated, the rest being shaded; or he could obtain the same reaction when the basal part was shaded and only a millimeter of the tip of the leaf was illuminated. In the former case, for aught we know, the whole process was local; in the latter, it certainly was not local. Yet there is no doubt in our minds that the processes were the same in both cases. In both cases there were excitation, conduction, reaction; only in the latter case, the excitation was in a different part of the plant, and the conduction was over a greater stretch than in the former. Yet it is over the differences which these two illustrations show that the controversy has arisen over *direct* and *indirect* response. A case

known to occur in plants seems to me to illustrate fairly well the so-called *direct* response of the zoologists: The leaves of some plants roll up when illuminated by the hot sun, due to the loss of water on the illuminated side. This is certainly *direct,* but most biologists would call it a mechanical, and not a sensitive response.

It has already been said that botanists accept the *indirect* method as applying in all cases to plants; and almost all zoologists take the same view with regard to animal reactions. We may conclude, therefore, that the term "tropism" may be used in the same sense for both plants and animals. The "tropism" resulting from direct action has not yet been demonstrated for either plants or animals. This conception of the significance of the term "tropism," as presented in the foregoing paragraphs, is not simple, but very complex; and in attempting to analyze the behavior of organisms, we meet with several conditioning phenomena, some of which may now be described. The terminology used in the following paragraphs is taken mostly from the zoologists, and botanists will note that the same terms are applicable to plant response.

One of the most widely extended of these observed phenomena is the variability of the response when the same external conditions are operating. Thus, Strasburger found the swarms-cells of *Ulothrix* and other algæ, during their early active period, positively heliotropic, but negatively heliotropic during their later active period. The change in *disposition* of the peduncle of the poppy, of the *Narcissus,* and of the members of various other plants, is familiar to all botanists. All of the foregoing changes in disposition can be referred, for want of a clearer understanding, to internal changes incident to age. These internal conditions which influence the response to external stimulus are called also the *physiological state.* The foregoing examples are illustrations of the influence of *physiological state* on response.

The physiological state may also be altered, and hence

the reaction of the organism may be altered, by an external agent which is not the stimulus to response. The rhizomes of *Adoxa* and *Circæa,* in normal surroundings growing horizontally because of their diageotropism, become positively geotropic when exposed to light, and grow toward the earth. The rhizomes of some other plants, in similar treatment, become negatively geotropic. Experiments have shown that these changes of direction in growth in these rhizomes are not heliotropic, but due to a change in disposition toward gravitation. Light does not cause the bending, but changes the physiological state, and gravitation causes the bending. Another illustration of a change in disposition due to external agency is furnished by the behavior of seedling peas and vetches which become more heliotropic when the atmosphere contains small quantities of illuminating gas, or of carbon monoxid. Loeb found that *Volvox,* some crustacean copepods and other organisms, are rendered more responsive to light by putting a weak solution of carbon dioxide, acetic or hydrochloric acid, in the water in which they are swimming. This author suggests that this influence on the physiological state[3] is due to the acid preventing the formation in the organism of some anti-positive substance, normally generated. This hypothesis may not be supported by future study, but there is some evidence offered in its behalf, and it is a worthy attempt to come a step nearer to the intimate processes.

The "trial and error" hypothesis as applied by Jennings to some phenomena of behavior in protozoa is defined by him as "the selection through varied movements of conditions not interfering with the physiological processes of the organism."[4] The term itself, "trial and error," has lately been abandoned by Jennings,[5] but the value of the hypothesis as describing behavior he still maintains. It is plain to see that the so-called direction movements, or tropisms, as they have been generally

[3] *Archiv f. Physiol.,* 115, 1906, 564.

[4] "Behavior of the Lower Organisms," 1906.

[5] AMER. NATURALIST, October, 1909.

recorded for our fixed plants, can not have their behavior included in this category; for by them there is apparently no *selection through varied movements.* Our typical plant tropisms show that one movement or curve, and that is unvaryingly toward the assumption of the new position of equilibrium. The response is what Bohn has called *resistless.* The term is expressive, and may be useful; but we must not forget that all reactions of lower organisms are resistless.

There are recorded, however, the results of two series of experiments with plants which seem to me to range themselves with the phenomena described as "selection through varied movements." I refer to the establishment of half-hourly geotropic rhythm in the stems of *Taraxacum* and valerian, and of quarter-hourly heliotropic rhythm in the cotyledons of *Phalaris* and *Avena,* by the work of Francis Darwin and Miss Pertz. If there is doubt as to whether the rhythms just noted illustrate the first part of Jennings's hypothesis for the description of the origin of behavior, namely, "the selection through varied movements of conditions not interfering with physiological processes," there can, I believe, be no doubt that the establishment of these rhythms illustrates the second part of the hypothesis, namely, that the "resolution of one physiological state into another becomes more rapid after it has taken place a number of times." The gradual shortening of the period of oscillation, in the plants used by Darwin and Pertz, till the half-hourly or quarter-hourly rhythm was established, seems to me to express the more rapid resolution of one physiological state into another.

Though the idea of trial and error seems capable of application to but few of the recorded reactions of fixed plants, it is descriptive of the movements of bacteria, swarm-cells and spermatozoids. For these plants, by varied movements, finally arrive at a condition of the environment which does not interfere with their physiological processes.

Another descriptive for a group of phenomena in behavior, used in both botany and zoology, but in quite different senses, is *differential sensibility.* Pfeffer applies this term to all of the tropistic processes of plants, including the typical tropisms and the shock-movements; and it is, as he says, true that it is only by a perception of difference in the stimulus on the two sides of an organism that we obtain any tropism. On the other hand, Nagel uses the same term—Unterschiedungsempfindung—in application to the shock-movements alone. Jennings, I believe, uses the term in Pfeffer's sense, Loeb and Bohn with nearly the same meaning as Jennings's *trial* and *error* idea, or, at least, they would claim that the *trial* and *error* phenomena are a combination of tropisms and responses to *differential sensibility.*

To Summarize: In considering the foregoing phenomena, only the so-called *direction movements* of fixed organisms and the locomotory movements of free-swimming organisms have been referred to.

The organisms considered—plants and protozoa—have no nerve-cells, but nevertheless, their reactions are, and may be, spoken of as *non-nervous reflexes.*

While the responses in *fixed* and *free-moving* organisms are different in their external manifestations, the relations of stimulus and response and the conditions of operation of stimulus and response are much the same in both classes of organisms.

The terminology as introduced and generally used by botanists has been chosen as mere designation of the obvious stimulus and the direction of movement of the organism. Hence *tropism* or *taxism* is used to designate all the responses which animal biologists, with closer attention to details of behavior, have subdivided into a larger number. In botany, therefore, the term *tropism* should be used in a more restricted sense than at present.

In both plant and animal behavior, this term may be restricted to those simple movements which result in

placing the organism in a certain direction with reference to the direction of the stimulus.

The term *fright-movement* or *shock-movement* or *recoil* (or a still better one) may be used to describe those responses due to a sudden change in the environment. Some of these shock-movements are doubtless tropisms, but perhaps not all. These are the movements that are due to differential sensibility (Unterschiedungsempfindung) in the sense of Loeb, and to transition stimulation (Uebergangsreizung) in the sense of Pfeffer.

There might also be some designation for the series of responses which Jennings attempted to name as "trial and error," a complex of tropisms and shock-movements, influenced by a varying physiological state.

Very recently Bohn has proposed to account for all behavior of lower organisms under four designations: *mechanical reflexes* (tropisms), vital rhythms (a group of *autonomous movements* of the botanists), *differential sensibility* and *associative phenomena.*

The ideas contained in these terms are all illustrated by plant behavior. But the terms are inadequate, for they are not coordinate. Some of them refer to responses, some to physiological state.

Before closing, reference might be made to Semon's book, "Die Mneme," the ideas in which, especially regarding *associative phenomena* in behavior, aid one in gaining a possibly clearer conception of the origin of some reactions of organisms.

Besides the reactions treated in the foregoing pages, for which a harmony has been attempted between the students of plant and animal behavior, we all know that there are groups which need a better and more expressive terminology than now is in use. As an illustration of phenomena needing more precise terminology, I might refer to the reactions known as epinasty and hyponasty. A very complete and apparently adequate terminology for all sensitive, non-nervous, reactions is given by Massart in *Annales de l'Institut Pasteur,* 1901, and a translation of the same in *Biologischem Centralblatt,* 22, 1902, 9.

THE LARVA AND SPAT OF THE CANADIAN OYSTER

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II. THE SPAT

IN the first part of this article, dealing with the larva,[1] I have already indicated that, in the progress of my research, it soon became necessary to plan means of procuring young oyster spat for comparison with my supposed oyster larvæ before I could feel satisfied that the latter were in reality larvæ of the oyster. Of the common bivalve mollusks only Ostrea and Anomia live fixed to objects of support, so that the matter has some appearance of simplicity in the fact that all free-living forms may be eliminated. But careful examination of eel-grass, rock-weed and other marine plants, of shells, stones, timbers and other objects revealed no young spat, and I was forced to wonder where the oyster secreted itself at this stage of its life. I examined sand with the microscope to find if, like many bivalves, the young oyster might burrow for a time, but with no better result. Bundles of brush were tied to submerged rocks, or weighted with stones and sunk at various places. These were examined at intervals but without success. Each failure suggested some new possibility that required examination and occasioned delay. Time was flying, it was getting late in the season, and each day brought no further progress. What stupendous obstacles present themselves to the investigator and how simple after one has once mastered them!

A copy of Jackson's work,[2] procured for me at this time by Professor Wright, was particularly opportune, and I owe to it much by way of information and suggest-

[1] AMER. NAT., XLIII, Jan., 1909, pp. 31–47.

[2] See literature 12 of part I.

EXPLANATION OF PLATE

The plate accompanying "I. The Larva" was intended to be lithographed of the same size but was reproduced smaller and lost detail. I find from measurements the figures are magnified about 30 diameters. To agree with it the figures 1, 2, 3 of this plate, "II. The Spat," are magnified 30 diameters.

FIGS. 1, 2, 3. Young spat of Canadian oyster from the right (upper) side as they occur attached. Magnified 30 diameters.

FIG. 1. Oyster spat .5 mm. high, showing larval and spat shells.

FIG. 2. Spat 1 mm. high. The larval shell grows no larger, the spat shell grows to the adult size. Many organs are sketched in but the liver is left out, as it would obscure other parts.

FIG. 3. Spat 1.5 mm. for comparison.

FIGS. 4–12. Transverse sections of oyster spat 1 mm. high (compare Fig. 2), viewed from behind so that left and right of the figures correspond with the observer. The sections are in order from anterior to posterior but are not successive. The shells had been decalcified and are somewhat diagrammatic, thin left and thick right valve.

FIG. 4. Section through region of upper lip and transversely to anterior filaments of left inner hemibranch.

FIG. 5. Through mouth, unmarked parts same as preceding. The lower lip is borne by the anterior end of the abdomen (region of the foot).

FIG. 6. Mouth open at right, closed in to œsophagus at left. Rudiments of upper and lower palps.

FIG. 7. Œsophagus and tips of filaments of right inner hemibranch.

FIG. 8. Abdomen with five liver-follicles about the œsophagus.

FIG. 9. Through center of stomach showing œsophagus about to enter it, origin of intestine and right and left stalks of liver. Three other liver follicles are shown as well as the inferior lobe of the stomach, the visceral ganglia and the left inner hemibranch.

FIG. 10. Through anterior edge of adductor muscle, posterior end of gill.

FIG. 11. Through adductor and tip of inferior lobe of stomach. Several liver follicles.

FIG. 12. Posterior edge of adductor with rectum descending.

FIGS. 13–18. Transverse sections of spat 2, 2.5, 3, 3.5, 4, 5 mm. high. Not equally magnified. Left valve often damaged or left attached.

FIG. 13. Through mouth of 2 mm. spat, showing labial palps.

FIG. 14. Section of 2.5 mm. spat, touching anterior edge of adductor, showing the supra-branchial slit leading out from the supra-branchial cavity on the right side and the rudiment of the right outer hemibranch. Right and left inner filaments are cut longitudinally.

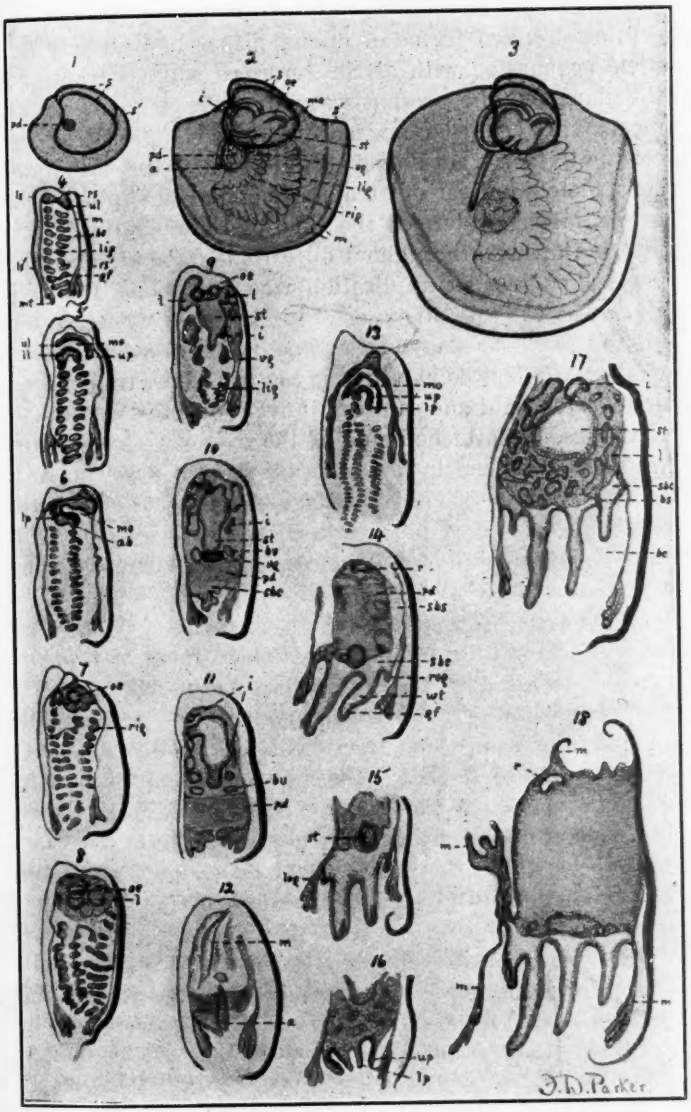
FIG. 15. Similar section of 3 mm. spat but slightly in advance and cut short above, showing rudiment of left outer hemibranch.

FIG. 16. Slightly behind mouth of 3.5 mm. spat, cut off above, to show all four labial palps. Liver follicles and portion of stomach above.

FIG. 17. Through 4 mm. spat, showing septa between supra-branchial cavities of inner and outer hemibranchs, the position of the original ctenidial axis.

FIG. 18. Section of 5 mm. spat through adductor muscle and visceral ganglia. The upper free edges of the mantle right and left of the rectum are very irregular. The branchial septa stop short of this section so that the supra-branchial cavity is continuous above all four hemibranchs.

a, anus; *ab*, abdomen; *bc*, branchial chamber; *bs*, branchial septum; *bv*, blood vessel; *gf*, gill filament; *i*, intestine; *l*, liver, *lg*, left inner hemibranch (gill); *ll*, lower lip; *lp*, lower labial palp; *ls*, left valve of prodissoconch (larval shell); *ls'*, left valve of dissoconch (spat shell); *m*, mantle; *mo*, mouth; *mt*, mantle tentacle; *oe*, œsophagus; *pd*, posterior adductor muscle; *r*, rectum; *rg*, right inner hemibranch (gill); *rs*, right prodissoconch; *rs'*, right dissoconch; *s*, prodissoconch; *s'*, dissoconch; *sbc*, supra-branchial chamber; *sbs*, supra-branchial slit; *st*, stomach; *ul*, upper lip; *up*, upper labial palp; *vg*, visceral ganglia; *wt*, water tube.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J. D. Parker

iveness. The method of putting out glass[3] for the reception of fixed forms of animal life I had already become acquainted with at St. Andrews while working on the clam, but the present was the occasion to try every means that could be devised and quickly applied. I accordingly took what objects could be easily procured and constructed and set out traps calculated to capture full-grown larval oysters at the time of their fixation. The idea is the same throughout all forms of the method; the particular turn in application was my own. Window-glass was cut into strips 2×6 inches so as not to be too big to use on the stage of a compound microscope, the advantage of glass being that one can use either transmitted or reflected light and can turn it over so as to see, through the glass, the attached side of the oyster. These strips were stood on end in deep crocks, about a dozen in each crock, and kept from falling against one another by wire racks, the object of placing them vertical being to minimize the aggregation of sediment on their surfaces. The traps were then planted at various places where there were oysters—off Curtain Island where the oysters were large, and off Ram Island Point where there were many sizes of young oysters. The crocks were sunk in gravel just below low-tide level and made secure against the buoyant force of water and the lateral action of waves and currents by building stones around them but leaving the tops open. It was thought that larvæ, either swimming about or swept about by the waves, might drop into the crocks where the water would be comparatively still and find it easy to cling to the glass during the first stages of fixation.

Ram Island Point appeared to be the most favorable place and that was about six miles from the station, but daily visits were made, the strips of glass were one by

[3] Ryder, Comm. Fish. Maryland, 1881, p. 57; Bull. U. S. Fish Comm., 1882 (1883), p. 383. Horst, Bull. U. S. Fish Comm., 1882 (1883), p. 165; Rep. U. S. Fish Comm., 1884 (1886), p. 906. Möbius, *Zool. Anz.*, Jan. 22, 1883. Winslow, Bull. U. S. Fish Comm., 1884, p. 354. Jackson, *Science*, 1888, p. 230 (Vol. XI, No. 275); *Mem. Bost. Soc. Nat. Hist.*, 1890, p. 285.

one withdrawn and examined with a lens, and whenever a suspicious looking speck was observed the glass was put in a pail of sea-water and taken to the station to be examined with a compound microscope.

The strips soon became dirty, receiving a slimy coat speckled with sediment, plants and animals. There were bacteria, diatoms, algæ, protozoa, sponge-spicules, hydroids, polyzoon-colonies, worm-larvæ, crustacean larvæ, small snails, etc. It seemed as if everything but oysters could be obtained. So far as I saw, I had neglected nothing that might contribute to the result in view. Could it be that my suspected larvæ were not oysters, that there were no oyster larvæ or oyster eggs in the water! Once more I was bewildered.

At length, on the sixteenth of August, I discovered a single minute oyster-spat, bearing unmistakable marks of recognition and enclosing within the lately deposited spat-shell the prodissoconch of the free-swimming larva. On the nineteenth I found a second (Fig. 3), and on the twenty-second a third (Fig. 1). Everything speedily became clear. My experiments had been running ahead of nature. Oyster larvæ had been in the water, but they were not ready to transform into spat. They had to wait their time. On the thirty-first of August a fourth was taken.

After finding the first oyster-spat on glass I at once directed increased attention to natural marine objects and on the second of September I found a spat on the surface of a half-grown oyster-shell. From this time forwards they were to be found in increasing numbers and on various objects and, after being once shown them, the deck-hands of the steamer *Ostrea* could also find them. I have found spat on the shells of the oyster, mussel, clam, quohog, bar-clam, razor-clam, round whelk and on stones, but they must occur on many other objects as well. Judging from the numbers of half-grown oysters that carry periwinkle-shells at their umbos, it would seem that the periwinkle is a common base of fixation, although I did

not succeed in finding any with young spat attached. The dark color of the winkle, of course, makes it easy to overlook the smallest spat, and besides, these shells are frequently speckled or spotted with plant colonies such as *Ralfsia verruscosa,* the small colonies of which may simulate young oyster-spat in size, shape and color. One can distinguish the difference with a lens or by feeling them with a knife-blade. The young of *Crepidula formicata,* a low conical-shelled gastropod, is sometimes more difficult to distinguish, but with a knife-blade one can slide it along the base of attachment or pry it off and note that there is no under shell but a broad clinging and creeping foot. Anomia is one of the closest relatives of the oyster, but, from its shape and color, is usually not difficult to distinguish. Upon prying it off, the thin lower valve of the shell can be seen to have a hole through which a short stalk of attachment passes and permits movement. The oyster becomes fixed by means of a secretion, presumably from the edge of the mantle, which cements the left valve close and fast to the supporting rock or shell.

The spat caught on glass did not, of course, occur in regular order of progression in size: the first measured .87 × 1.03 mm. in height and length, the second 1.58 × 1.20, the third .51 × .55, the fourth .86 × .95. Similarly the first found on an oyster shell measured 2.4 × 2.3, while those subsequently procured varied from less than 1 mm. to 6 mm. in height.

The shell of the larva is longer than high, and this is true not only for each valve but also for the whole shell, even when the far umbo, through tilting of the shell, stands up above the near one. The youngest spat agree also with this statement, but when about 1 mm. in height the proportions become reversed, and from this time forwards the shell grows fastest below and at the postero-inferior angle. On this account it is more useful at first to build comparative measurements on the height rather than on the length—the height, both for the larva and for

the spat, being the vertical measurement from the top of the umbo to the lowest level of the opposite edge when the prodissoconch is placed in the position of a creeping clam.

The spat caught on glass exhibited the characteristic color of the pelagic larva—the smallest varying towards pink, the larger towards brown. Those taken on opaque objects, on the other hand, presented a different appearance—instead of having a pink, reddish or brown coloration as one would expect from comparison with the larva, or, instead of having a white appearance as might be looked for by comparison with the older spat and adult oysters, they preserved a shining, dark, metallic lustre with a few faint radial lines. In the center of the dorsal region could be distinctly recognized the larval shell (prodissoconch) of the oldest free-swimming stage, presenting a uniformity of appearance in all the specimens, and measuring in the neighborhood of .369 × .384 mm. in height and length.

The spat-shell (young dissoconch) is deposited by the thickened rim of the mantle in layers along the ventral and terminal edges of the larval valves, but not to any extent along the dorsal or hinge edge, which explains the concentric lines below the umbos. The latest deposited parts around the margins are very thin and delicate and exhibit a prismatic structure. At first the shape varies little from that of the prodissoconch, but soon the dissoconch becomes extended fore and aft of the hinge-area in a manner that suggests the wings (ears) of a scallop-shell, the lower parts preserving a pretty uniformly curved outline. Later these alæ cease to be conspicuous and the whole outline may become irregular and variable. Deep or shallow concentric creases preserve more or less indication of stages of growth, and at places may be portions of radial lines. The deeper concavity of the left valve remains noticeable for a time after fixation takes place, particularly in sections, but a little later the lower valve seems to lag behind the

upper one in growth, appearing thinner and flatter, while the upper one is thicker and more curved. At a still later period the growing edge of the lower valve becomes free and the valve again acquires a deeper cavity than the upper one, preserving this difference throughout life.

While the developing oyster is free to swim or to creep it is, of course, natural to describe it in terms suitable to such permanently free-living species as the clam. The more pointed end, that ordinarily precedes in locomotion and from which may protrude the velum or the foot, is the anterior end. The foot is postero-ventral to the velum. The umbos are postero-dorsal. The hinge is dorsal, *i. e.*, between and in front of the umbos. The longest diameter is horizontal, and the height is a vertical line at right angles to the length. With the growth of the spat it becomes difficult to retain such ideals as continuously useful marks of description. At periods varying somewhat with the individual they become more or less modified. Preserving the original orientation of the prodissoconch, the height of the dissoconch soon becomes greater than the length, the hinge and umbos come to mark the narrow anterior end of the spat, and the larval shell sinks into insignificance. Its left valve frequently becomes obliterated by growth of the surface of attachment, but its right valve may often be found until late in the life of the spat, although it is liable to become destroyed by weathering of the umbo-region. While its position marks the anterior end of the oyster, it has long since been carried up on the tip of the umbo of the dissoconch out of reach of the hinge or of the growing parts, but its anterior end still points in a general way in the direction of the anterior end of the adult. This position and relationship is correlated, as will be seen later, with the increase of growth of the lower and posterior parts of the oyster's body, which occasions more or less of a rotation round the great adductor muscle, and resulting in longer or rounder forms of shell with a straighter dorsal and a much curved ventral border.

The right, upper, valve remains flatter and smoother, the left, lower or attached valve, more deeply hollowed, rougher, with more conspicuous concentric furrows, and often with blue tipped projecting processes.

Note on the Asymmetry of the Shell.—In the free-swimming larva the greater convexity of the left valve can not be due to external conditions in the life of the larva since both valves are developed under like conditions, but must result from a cænogenetic modification of biogenesis, which is to say that the difference in the two valves was first developed after some remote but free and symmetrical ancestors of the present oyster took to a fixed mode of life, becoming attached by simply cementing the left valve fast to a solid substance upon which it rested, and that somewhat later in the phylogenetic development the hereditary transmission of this character became modified to precede, in the life of the individual, the conditions which originally called it into existence. It is conceivable that gravity was the prime incentive both to the occasion for fixation on one side and to the first asymmetry. Many other mollusks have been similarly modified, *ē. g.*, Anomia, Pecten, Mya, deep-bodied animals that habitually fall over on one side as soon as locomotion ceases. When once developed there may have been an advantage in transmitting the lob-sidedness to earlier and earlier stages in the offspring, which could take place by natural selection. Such an advantage might well be the determining that the heavier left side of the larva, when settling to the bottom or when creeping movement ceases, should promptly come in contact with the point of fixation and insure the most favourable relative positions for the activity of other organs whose function had been perfected under like conditions in the adult. The temporary transfer of the greater convexity to the upper valve in young stages of the spat can be explained by the fact that for a time the growth of the lower valve follows, as it is cemented to, the surface upon which it rests, while the upper valve is free for growth in every direction. When a sufficient surface of attachment is secured the edge of the lower valve becomes free, and then the greater convexity soon reverts to the left valve again.

In living spat the mantle can be often seen protruding beyond the edge of the shell, but in preserved specimens it is retracted, sometimes close up to the gills and body, so that the soft parts of the animal may occupy only a half to a third of the cavity of the shell. In the youngest stages the margin of the mantle is thickened, and the beginnings of tentacular processes are present. Differences in the two sides afterwards become noticeable, such

as thickness, length, and the greater freedom of the right side from the body, where, for a considerable area in front of the adductor muscle, there is open communication from the supra-branchial chamber to the outside at the dorsal edge of the shell (Figs. 14, 15).

The anterior adductor muscle is present for a time in the spat, and appears to move upwards and backwards from its original position in the larva, until it is crowded to the edge and disappears before the oyster reaches 1 mm. in depth. The posterior adductor muscle, on the other hand, increases regularly in size and moves downwards and slightly backwards, leaving distinct lines on the shell to indicate its change of position. In spat .86 mm. high it is just below the edge of the prodissoconch (Fig. 2), in those 1.5 mm. high it is twice the depth of the prodissoconch from the top of the shell (Fig. 3); in all stages it is nearly in the median horizontal plane and slightly posterior to the median frontal plane. The movement may be effected by a slow creeping of the muscle, due to downward pressure from the growth of the body above, or by the addition of new fibers below and the absorption of old from above, while the impressions on the shell may result from the inability of the mantle to deposit new layers of pearly matter under the attached ends of the muscle.

Of the organs enclosed by the mantle a conspicuous part is early assumed by the gills. The oldest larva or the youngest spat has two of these—one on each side of the body, below and between the line of attachment of the mantle and the base of the foot. At this time each gill possesses a row of about eight filaments, of which the anterior are larger and more completely separated from each other, the posterior are shorter and only partly separated by vertical creases, while all are united above by an undivided longitudinal ridge or basal axis that projects behind and below the mass of the body. At the time of fixation the right and left gills are approximately equal, but when the spat reaches .86 mm. in height (Fig.

2) there are about sixteen long filaments on the left side and about ten short filaments on the right side—the left gill extending in front of and behind the right one and occupying most of the gill-chamber (Figs. 4–8). In spat of 2.5 mm. height there appears on the right side, outwards from the already present gill, a third series of minute, papilla-like filaments (Fig. 14), and when the spat reaches 3 mm. in height a fourth series is to be seen in the corresponding position on the left side (Fig. 15). They increase in size during the growth of the spat until the animal possesses four complete gill-leaves corresponding with those of the adult.

During larval development the gills of the oyster make but little progress towards the complicated structure of the adult. The free-swimming animal being small, respiration can for a time be partly subserved by its surface. But fixation effects a marked change in its mode of life and is followed by far-reaching modifications in its organization. Rapid increase of size demands improved facilities for respiration. But, as the animal no longer comes in contact with its food through swimming movements, it must depend upon the respiratory currents for bringing food to itself; hence the gills acquire a double importance. Moreover, since the conditions favorable to bilateral symmetry are interfered with, the equal balancing of right and left sides in the further growth of organs must be left to heredity. At the time of fixation, as we have seen, the gills are represented by two bilaterally symmetrical inner gill-leaves. The left (now under one) grows much faster than the right (now upper one) so that there is more room and less pressure above, facilitating the development of the right outer gill-leaf before the corresponding one of the left side. Irregularity also soon becomes noticeable in the higher level of origin of those of the right side and in a tendency towards a radial symmetry of the organs with reference to the posterior adductor muscle.

A study of sections of larvæ and young spat reveals

a remarkable difference in the apparent ontogenetic development of the gills of the oyster as compared with the recorded phylogenetic development in lamellibranchs. This, like the larval asymmetry of the shell, may be understood as a short-cut towards the final structure. As the first-formed, short, basal axes grow backwards they carry with them a continuation of the body-wall, connecting them with one another across the median sagittal plane and with the mantle at both sides, giving rise to a very imperfect separation into branchial and supra-branchial (or cloacal) chambers. The filaments are at first short, solid, papilla-like outgrowths from the axes —the older and larger anterior, the younger and smaller posterior. They originate behind, but by formation and growth of new ones those first formed become pushed forwards. The at first small and shallow supra-branchial chamber follows this movement and penetrates each filament from above, distending it laterally but not antero-posteriorly because of the pressure of contiguous filaments. This process continues until each filament is severed into an outer and an inner section, the intermediate portion becoming constricted through, but never completely at the tip. In this manner each gill-leaf becomes split into outer and inner lamellæ of similar structure, but the one the reverse of the other, with its parallel half-filaments and intervening slits overhung by cilia. Imperfect separation of the transverse median portions of the opposed halves of some filaments gives rise to the inter-lamellar junctions, while the imperfect separation of the opposed sides of different but contiguous filaments occasions the inter-filamentar junctions. The same process can be observed later in the development of the right and left outer gill-leaves as well as in the terminal filaments of any one of the four (Fig. 14).

For a long time it has been customary among zoologists to speak as if the oyster, or other bivalve mollusk, possesses four gills, which it really appears to do, two on each side of the body. Comparative study of the anatomy and of the development of different groups has led to the

view that bivalves have been developed from primitive, symmetrical, gastropod-like ancestors, with a simple head in front bearing two tentacles, two eyes, and mouth with a rasping tongue; a low conical shell above that could be drawn down over all the soft parts and lined by a mantle that secretes its material; a flat creeping and clinging foot below; and two feather-shaped gills, disposed right and left, projecting backwards. Each of these was a symmetrically constructed, bipectinate gill or ctenidium, having a central axis with two rows of filaments, an upper and a lower. There are still living limpet-like gastropods along our coasts possessing such characters, although no one species retains them all or in the most primitive form.

The group of mollusca to which the oyster belongs has in the course of time suffered modifications of the characters mentioned. Its members have taken to a more quiescent mode of life, such as burrowing in sand or fixing to rocks, and in consequence have largely lost those external organs of locomotion, plunder and special sense so necessary to free-roving animals. The absence of a head has been regarded as characteristic (hence the group has been called Acephala); in place of a single piece they have developed a shell with two valves (Bivalva); the foot in by far the greatest number of forms has become somewhat hatchet-shaped (Pelecypoda); the gills are leaf-like, each separable into flat plates (Lamellibranchia). If all bivalves had become equally modified it would certainly have been difficult to determine the origin of the group, but, owing to the diversity of natural conditions and the reactions of these upon living organisms, certain species have been forced to pursue special lines of action in order to better their chances for life, with the result that the organs chiefly concerned have become more specialized, while other organs have retained much of their original structure, and it is just these organs that are especially valuable in tracing ancestral affinities. As long ago as 1848 Leuckart (16) comprehended the essential unity of molluscan gills, and his views have been supported by Menegaux, Pelseneer, and many others. Peck has studied the Lamellibranch gill. Lankester, Hatschek, Thiele, Lang, are among those who have studied the phylogeny.

In the oyster larva one can at once recognize the ctenidial axis with its lower series of filaments, but one has to await the spat of 2.5 to 3 mm. before he can see the upper series, which has had to rotate outwards nearly half way round the axis in order to remain accommodated in the branchial chamber. In the adult there is but one gill on each side, comparable with a gastropod ctenidium and composed of two hemibranchs (gill-leaves or branchial foliæ); each hemibranch may be split lengthwise, from above nearly to the lower free edge but not through it, into outer and inner plates (lamellæ), or subdivided transversely into numerous V-shaped branchial filaments of which one half

belongs to the outer lamella and the other half to the inner lamella of a hemibranch.

In the course of phylogenetic development the originally straight filaments have become bent upon themselves to permit of greater length (surface) and still be protected within the branchial chamber—those of the ventral series were folded inwards and those of the dorsal (but now lateral) series were folded outwards, while the tips coming in contact with the foot in the one case or the mantle in the other clung for support, were directed upwards, and finally became fixed along the side of the body or along the inner surface of the mantle. At places their ciliated surfaces became knit together for further support, leaving intervening gill-slits between contiguous filaments, and ascending water-tubes between opposite lamellæ. At the level of union of the gills with the body and with the mantle there is separated off a branchial chamber below from a supra-branchial (or cloacal) chamber above, and by the activity of the cilia water is brought into the former, directed through the gill slits, up the water-tubes, and out by the cloacal chamber. The original ctenidial axis lies above the base of origin of each pair of hemibranchs, and is marked by retaining its connection with the body by a septum carrying blood vessels and nerves (Fig. 17).

Two larval organs soon disappear under the new conditions brought about by fixation: the velum and the foot. Even in certain old, free-swimming larvæ, that are perhaps belated in their efforts to become attached, a reduction in the size and vigor of the velum is noticeable. This would seem to suggest an atrophy of the organ, which might be followed by either dehiscence or absorption. I have occasionally seen old larvæ with the velum protruded and partly severed from the body, as well as completely separated vela still capable of muscular and ciliary movements. Such cases may have resulted from accidental pinching off by a snapping closure of the shell-valves. But the size, appearance, enfeebled movements, and even the accident itself, pointed towards an antecedent loss of ability to respond correlatively to the activity of neighboring organs.

Balfour (21, p. 215) states: "It has been suggested by Lovén, though without any direct evidence, that the labial tentacles of adult Lamellibranchiata are the remains of the velum. The velar area is in any case the only representative of the head."

Ryder (31, p. 404) says: "The detachment of the ring or crown

of vibratory filaments or cilia from the embryo as asserted by Davaine has not been confirmed by any other observer" and in 8, p. 790: "Davaine makes the statement that the velum appears to drop off sometime about the end of the larval period. Gerbe, on the other hand, asserts that the velum is transformed into the palps." This is a fascinating view of the destiny of the velum: that it does not become entirely useless and completely disappear, that its main line of folding in the median sagittal plane represents the division into two halves which bend around the sides of the mouth, each half again folding to form the two palps, while secondary radial foldings may give rise to the furrows and ridges and the cilia become redistributed. On the other hand it is not easy to see exactly how an organ of the size and shape of the velum could become reduced, remodelled, changed in position and folded in such a way as to form an anterior pair of palps, connected across in front of the mouth, and a posterior pair, connected behind the mouth and underlying the first, while the two on one side are attached along a line running back from the mouth and have their original ciliated surfaces turned towards each other. Moreover, this would mean a much more intimate connection between the epithelium of the velum and the inner walls of the mouth than exists in the larva, where the mouth-opening is surrounded by a funnel-shaped projecting rim, that is separated from the velum in front by a crease, while the lower lip is free to a still greater extent. There is no observable connection between the arrangement of cilia on the velum and on the palps, nor any positive antecedents of the furrows and ridges of the palps on the velum. Besides, from a consideration of the size of the velum in the larva and the size of the smallest recognizable palps in the spat, it would appear that the velum would have to suffer a period of decay followed by a period of vigorous growth. Restricting one's observations to the oyster it might seem just as likely that the lower palps should originate from the foot and only the upper ones from the velum. The foot is ciliated and has a median ventral furrow corresponding with the division-line between the lower palps. In that case one would expect to find vestiges of pedal organs, such as pedal ganglia and otocysts, about the bases of these palps under the œsophagus, as well as supra-œsophageal ganglia in the bases of the upper palps in front of the œsophagus. But in my sections I have not been able to recognize these structures, and reflection on other bivalves, where both foot and palps persist as functional organs in the adults, proves beyond doubt that the foot has nothing to do with the lower palps. I have three series of young spat-oysters with the shell measuring rather less than 1 mm. in height, and from a study of them I should say that the palps originate from, and belong to, the walls of the mouth, *i. e.*, are extended upper and lower lips.

The foot, after fixation of the larva, no doubt ceases to grow, perhaps becomes reduced, but in any case shrinks against, is absorbed into and incorporated with the anterior ventral wall of the rapidly enlarging abdomen. In 1 mm. spat it is scarcely recognizable as a median, grooved, muscular thickening between the lower lip and the first gill-filaments.

Jackson (12, p. 303): "The fact that a velum, or swimming organ, exists up to the period of permanent fixation accounts for the great reduction of the foot, because that organ is unnecessary while the animal is provided with another locomotive organ, and is useless for progression after the animal is attached. The reduction of the foot is clearly attributable to disuse and a high degree of concentration of development . . . seen so markedly in the development of the oyster." I have already shown, when dealing with the foot of the larva, that the part designated "foot" by Jackson and others is not the real foot, which is only to be found at a very much later period and which they had not recognized.

The intestinal system has all its parts represented in the larva. With the growth of the spat these suffer certain alterations in relative sizes, shapes, and positions. Perhaps the most radical change is produced by a rotation of the body in such a way that the mouth moves forwards and upwards towards the antero-dorsal margin of the prodissoconch. This doubtless accompanies and is associated with the loss of the velum, which in the larva is so large as to occupy all the fore part of the cavity of the shell, forcing the mouth and œsophagus backwards to near the median frontal plane of the body. In spat under 1 mm. in height when the velum is completely cleared away, the mouth can occupy its normal position as in the adult. Such a rotation may appear at first thought inexplicable, but when it is remembered that in the prodissoconch the body of the larva is possessed of great freedom of movement, being at times thrust far forwards, putting the retractor muscles on the stretch, it can be readily understood. In fact it is conceivable that these muscles may be made to do duty in producing the rotation and in fixing the body in its new

position, for after the loss of velum and foot there is no longer any need of such free movement, consequently these muscles may lag behind other parts in growth, exerting a tension as they do so sufficient to cause the rotation. In harmony with this view is the similar upward movement of the anterior adductor muscle and the rapid downward movement of the posterior adductor muscle.

In 1 mm. spat the two sides of the mantle, meeting above at a broad angle, appear to be suddenly thickened (Fig. 4) into a sort of upper lip for the widely open, transversely crescentic mouth, that opens a little farther back on the right side than on the left. The anterior end of the body, between the first gill filaments, serves as lower lip, while very short upper and lower palps, possessing only a couple of ridges and furrows, are continuous with the lateral margins of the upper and lower lips, and project on each side of the anterior end of the median left gill. In 2 mm. spat (Fig. 13) the palps have increased perceptibly, doubled the number of furrows, turned down, and are seen to be anterior to, but not continuous with, the gills. Judging from the great progress made between these two sizes, I believe that the palps originate sometime before the spat reaches 1 mm. in height, but are not present as such in the larva, where upper and lower lips and palps are represented by the internally-ciliated, funnel-like, projecting rim of the mouth. When this rotates upwards it comes to lie between the mantle above and the forward growth of the abdomen below, while its side-angles fold outwards and backwards becoming the palps, their like surfaces turned towards each other and their cilia continuous with that of the mouth and œsophagus. Later they become adherent to a greater extent along the lateral walls of the anterior part of the enlarging abdomen, and direct food from the gills into the mouth.

Rice (33, p. 28) curiously made the observation: "During the first period of attachment when the shell itself is not firmly attached, but simply held firmly down to the substance with which it is in contact,

the young animal gets its food, or a portion of it, by means of a sort of proboscis, or elongation of the mouth part, which is capable of being moved about freely within the shell cavity. This proboscis stage lasts until the gills are fully formed and becomes of sufficient size to supply food to the animal, when the proboscis, or rather its flexible end, is transformed into the labial palps which become closely connected with the gill-leaves."

The mouth narrows down into an œsophageal tube of transversely elliptical calibre, lined by cells similar to those of the mouth. It is still relatively long and curves over the anterior end of the stomach, passes between the lateral origins of the liver, and enters the stomach from above (Figs. 2–10). The stomach is a relatively large mass of irregular shape and large cavity, occupying a good part of the space in the prodissoconch. There may be considered to be three prominent extensions: one forwards below the œsophagus, another postero-dorsal behind the entrance of the œsophagus, and a third, beginning as a compressed ventral extension of the first, slants downwards and backwards towards the adductor muscle, becoming broad, deep, regular and thick-walled. This, I am satisfied, is the portion that secretes the crystalline style, and originates postero-dorsally in the left umbo of the larva, but becomes moved to its present position during the rotation of the viscera, and presents the appearance of being internally ciliated. Just in front of the insertion of the œsophagus but on each side of it, *i. e.*, dorso-laterally, spring the stalks of the liver—one on the left and two on the right. These branch into numerous follicles lying on both sides of and above the stomach and projecting far forwards to the region of the mouth. On the ventral aspect of the stomach, in the same region, springs the intestine, on the right, in the crease between the compressed antero-ventral extension to the left and the main central body of the stomach above (Fig. 9). From this the intestine passes backwards on the right, then upwards behind the rounded postero-dorsal extension, forwards and down the left side, where, near the anterior end of the stomach it turns

backwards and then down, finally passing towards the median plane to the anal opening over the adductor muscle. The stomach sometimes contains diatoms and desmid-like clusters of one to four nucleated cells.

The nervous, circulatory, excretory and reproductive systems remain undescribed, and shall not be treated of in this paper; they bear less important relations to those characters of external morphology and gross anatomy that are so useful as marks of recognition and description.

The first, second and third spat oysters caught on glass were of different sizes and were consequently devoted to morphology, but the fourth, being of approximately the same size as the first, was used for a physiological experiment in growth. This spat was procured on the afternoon of August 31 at Ram Island, about six miles from the station, and measured at 5 P.M. .861 × .953 mm. in height and length and had about sixteen gill filaments. It was kept under the bridge of Keir's wharf until the afternoon of September 1 and measured again, but it showed no increase of size. It was then taken to Ram Island and placed under its original conditions in a crock, and at 4 P.M., September 7, it measured 1.276 × 1.261 mm. and had about twenty-four gill filaments. It was kept in running seawater until 5 P.M. of the eighth and then put under the bridge of the wharf until the morning of the ninth, when it was again taken to Ram Island. It did not grow either in the running water or under the bridge where there is at times considerable tidal current. On the forenoon of the sixteenth it was again brought in and measured 1.753 × 1.661 mm. From these observations it would appear that the young spat did not become immediately accommodated to new conditions after being disturbed, that during a period of six days of undisturbed growth it increased to one and one half times its original height, and that at the end of seven days more it had grown to twice its original height. One might say that it doubled its height and length in two weeks.

Having to leave for Montreal by the twentieth, it appeared that the best thing left for me to do was to plan an experiment for the winter. I had three strong wire baskets made—two feet square by three inches deep and lids to fasten over—in which I placed perhaps three to four hundred small, selected, living oysters having one or more minute dark spat upon each shell, surrounded with circular lead-pencil marks for convenience in recognition. These baskets were connected by a long rope and put down in a deep channel between Hog and Bird Islands, presumably out of the way of fishermen, ice-shoves, etc. I expected the small dark spat, which varied from 1 to 4 mm. in height, to grow to about the size of one's thumb-nail during the winter and spring, as this was the size of the smallest white spat I recollected having seen upon first arriving at Malpeque the previous spring. The first thing I did the succeeding spring was to go and grapple for these baskets, but despite every effort they could not be found. The marks of the rope and baskets could be observed on the bottom, and the suspicion was near that some curious fisherman, in setting lobster traps in the early spring, had found them and taken possession for the rope—an illustration of the immediate short-sighted petty-selfishness and improvident disregard of impending wholesale benefits of many fishermen.

The next thing that suggested itself was to look for spat of the previous autumn on the shells where I collected those for the preceding experiment, and I was surprised to find dark spat still there, that had apparently not grown a bit or changed in color during the winter. There were fewer of them—many having died and lost the upper valve or even both valves were gone, leaving sometimes a patch or rim to indicate where a spat had been attached. The largest dark spat collected the previous autumn measured 6 mm., and the largest found the next spring was 8 mm. in height. They retained their dark metallic luster with radiating ridges

or lines and very thin edges—the whole oyster being thin and fitting so solidly against the supporting shell as to require some force with a knife-blade to separate it. In some of the larger was to be seen a tendency to turn white, in that the dark rays were irregularly separated by reversed lighter radiations. Sizes but little larger than these may be found later in the spring and in the early summer. The spat of the oyster-fishermen, varying mostly over one inch in length, are abundant, many barrels of which are collected by the Indians at Ram Island Point and thrown out off Lennox Island, the Indian reserve, for further growth.

Important results added to those given in the preceding part on the larva are:

19. First systematic use of plankton nets in the procuring of oyster larvæ.

20. First undoubted recognition of the larva of the oyster in Canada.

21. Stages hitherto unobserved (constituting the blank referred to by Jackson) may be taken in the plankton net.

22. The first undoubted recognition of young stages of Canadian oyster spat.

23. The spatting period has been limited.

24. The free-swimming period of life of the larva has been limited.

25. Size is a more useful criterion than age.

26. Sections have been prepared of both larvæ and spat in order to determine accuracy of structure.

27. The gills have been carefully studied.

28. The intestinal system has been described throughout.

29. Development has been followed up to adult sizes.

30. Many structural or other observations have been made, which to enumerate would be largely to rewrite foregoing pages.

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BRIEF NOTES AND EXTRACTS

Ryder (I. The Larva. Literature, No. 6, f. 3) and Jackson (No. 12, ff. 1, 2, 17, 18) have given figures of the youngest stages of oyster spat.

In the absence from the literature of any figures of the oldest free-swimming larvæ, I have already referred to these and for a more satisfactory understanding reduced their measurements to actual sizes. They represent the spat within 24 hours after fixation and measure in the neighborhood of .3 mm. in height. Ryder's Figs. 5, 4, 6, 7, represent spat of about .34, .38, .51, .54 mm. height. Jackson's Fig. 3 was perhaps about .55 mm. high and his Figs. 20, 21, about .91 mm. high. Then come Ryder's Fig. 8, about 1.6 mm., his (No. 8, p. 784) Fig. 2 of 3 mm., and Jackson's Fig. 4 of 5 mm. My youngest spat were .51 and .86 mm. high and from 1 mm. upwards I had such abundance I could select whatever sizes I desired.

On account of recorded differences between European and American oysters it is not always safe for us to judge from analogies. On the other hand, except for local differences of temperature, food, fauna, etc., the accrued knowledge of oysters in the United States is of immense value to Canada.

Importance of Embryological Study.—Winslow (No. 30, p. 234): "I would press the importance of continued investigation of the embryological life of the oyster. The effects of the various influences to which it and the mature animal are exposed should be determined as early as possible. Knowledge of these influences and intelligent appreciation of their effects are absolutely necessary to the success of oyster culture. Thousands of dollars would be annually saved to the Connecticut oystermen if they could determine, with even approximate accuracy, the date when the attachment of the young oyster would occur. Hundreds of thousands would be saved if they had any reliable method of determining the probabilities of the spawning season. Careful, continuous, and elaborate study and investigation alone can determine these points and others of equal importance. Considering the value of successful determination, not only in a scientific aspect, but practically, no effort or expense should be spared to obtain it."

Spawning.—Winslow (29, p. 130), Tangier and Pokamoke Sounds: "The spawning season was said to be from May until August inclusive, though most of the spawning was done in June and July." Brooks (5, p. 10): "Oysters in from 1 to 6 feet of water in the vicinity of Crisfield, probably spawn between the middle and end of May, but oysters with ripe eggs were found in water from 5 to 6 fathoms deep from the first to the thirtieth of July, although most of them spawn late in June." Ryder (7, p. 326): "In the region of the Chesapeake the most important spawning period seems to extend over the months of June and July, but considerable ripe spawn may be found even much earlier and later than this."

Growth of Larva.—Ryder (7, p. 328): "At a temperature of 75 to 80° F. the period of incubation of the American oyster is only 5 to 6 hours, when the young commences to live an independent active existence." "The duration of the locomotive stage of development of the larva has not yet been certainly determined . . . it has been found by the writer that under favorable circumstances attachment of the fry probably takes place within 24 hours after fertilization as represented at *m* in Fig. 1. The young, however, after attachment, continue to grow as larvæ . . . when the valves of the fry have acquired umbos the development of the spat shell begins." Ryder (9, p. 728): "I would infer from what we learn from the study of other animals that it may require quite a week before an embryo reaches

the dimensions of 1/80 of an inch, but we have no data upon which to base any conclusions of value.''

Spatting.—Rice (34, p. 115): ''The attachment takes place in about two days from the time of fertilization.'' Jackson (11, p. 532): ''One of the most successful spatting grounds at Buzzards Bay is a sand spit on South Wareham . . . oysters were spatting most abundantly late in July and early August.''

Growth of Spat.—Ryder (9, p. 728): ''After fixation the growth of spat is very rapid—week or 10 dys., $\frac{1}{4}$ inch across; 20 dys., $\frac{1}{16}$ in.; 44 dys., $\frac{1}{8}$ in.; 48 dys., 1 in.; 79 dys., $1\frac{3}{4}$ in.; 82 dys., 2 in.'' Ryder (7, p. 328), Figs. 5, 6, 7, etc.

Number of Spat.—Ryder (32, p. 287): ''As many as 25 young oysters might have been counted on a surface of one square inch'' on wooden buoys taken up early in July near Woods Holl. ''More than 100 oysters on a single shell.'' Rice (34, pl. 6, f. 12) figures the inside of an old oyster valve with 165 young attached. I never saw anything like such numbers at Malpeque—having to examine many shells to find one bearing one or two spat.

Output.—Winslow (30, p. 233) gives for the United States 22,195,370 bushels, of which 19,712,320 bushels came from Chesapeake and Delaware Bays. Kemp (42, p. 353) gives for Canada a table from which it is seen the maximum production was reached in 1882 of 64,646 barrels.

Breeding.—Rice (34, p. 115): ''The first efforts in this country in the direction of artificial propagation were made by the writer in the summer of 1878 in conjunction with Dr. W. K. Brooks, but these experiments were not successful. The next summer, however, Dr. Brooks succeeded in impregnating the eggs and in raising the embryos until they were six days old.'' Brooks (5, p. 3): ''. . . succeeded in raising countless millions of young oysters.''

Oyster Culture.—Under this head might be included an extensive literature dealing largely with the transplanting of oyster spat, that have escaped the accidents of nature, to more favorable localities as regards crowding, competition, food, cleanliness, etc.; but also to a more limited extent the breeding of larval oysters under artificial conditions that protect them against extremes of temperature, violent storms, starvation, rapacity of animals, etc., and the furnishing of abundant and suitable objects for fixation. The subject is too vast for discussion in this place.

It would appear that, to some extent simulating the life-history of the oyster, the short period of activity in investigation and experimentation initiated by Brooks was succeeded by a period of quiescence in research, when statements were repeated but not examined anew. Deliberate, painstaking, self-reliant, and unbiased work, like that of Nelson (37), may do much to originate a new cycle of exact observation, which sooner or later may be turned to account in a rational system of oyster culture.

MONTREAL, May 18, 1909.

THE ALIMENTARY CANAL OF A CARBONIFEROUS SALAMANDER

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INVESTIGATORS, during the progress of their research into the anatomy of extinct animals, have the good fortune, from time to time, to be able to add items of interest to the soft anatomy of the forms which they are studying. In the nature of the case the soft parts are very rarely preserved and when they are represented it is usually an imperfect record. Occasionally, however, the rocks yield forms which afford very complete knowledge of the soft anatomy of the animal. This has been strikingly shown in Dr. Dean's studies on the fossil sharks of the Cleveland shales of Ohio. Dr. Eastman and Dr. Parker have also studied and described the soft parts of the head, especially, of a peculiar little fish from the Waverly shales of Kentucky which Dr. Eastman has named *Rhadinichthys deani*. In this species, which is represented by an abundance of material, there are clearly preserved the various portions of the internal ear, the outlines of the lobes of the brain and traces of an arterial blood vessel with some of its branches. There are many other instances in which the soft anatomy of fossil fishes has been developed. Many of these are given more at length by the writer in another place.

Among the higher vertebrates the softer structures are not so well known. The outlines of various branchiosaurians are known from the studies of Fritsch, Credner, von Ammon, von Meyer and Thevenin, who have described these forms from the Permian and Carboniferous of France, Bohemia and Germany. Cope has dwelt at some length upon the preservation of the shape and some of the coloring matter of the eye of the reptile-

like microsaurian, *Amphibamus grandiceps,* from the Mazon Creek shales of Illinois. The writer has been fortunate in observing the outline of the body of this species. He has also observed muscle fibers in the abdominal wall and the outline of the body in *Tuditanus walcotti* from the Coal Measures of Ohio. He has described, also, the fin membranes, the lateral line organs, the form of the body and the "pigmentum nigrum" of the eye of *Micrerpeton caudatum* from the Mazon Creek shales. Dollo has described an unusual amphibian from the Wealden of Bernissart, Belgium, *Hylæobatrachus croyii,* which showed the preservation of some of the body membranes and thus a portion of the form of the body. Numerous observers have written on the form of the feet in amphibia as they have been recorded by their footprints in the rocks.

Nothing has ever been contributed to the structure of the intestinal tract of the fossil amphibia, and from the nature of the case as well as from the extreme rarity of approximately complete specimens of these animals it would be an unexpected event if such were discovered. Our confidence in the preserving powers of the rocks grows, however, from year to year, and if we look long enough we can not fail to uncover many things of interest.

The amphibia of the Mazon Creek shales have always been noted for the unusual perfection of their preservation, which they have shared with other animals and with the plants from that historic locality. *Amphibamus grandiceps,* the first amphibian described from these shales, was made known in 1865 by Professor Cope from an almost perfect specimen. The next species made known from these shales was the form described in 1909 by the writer under the name *Micrerpeton caudatum.* It was based on a specimen which lacked only portions of the limbs of being complete. Nothing of the intestinal tract was observed in either of these species. It was somewhat surprising, on that account, to observe among

a lot of specimens loaned the writer for study by Yale Museum, on two excellently preserved examples of the Branchiosauria, apparently adult, molds and impressions of what appeared at first sight to be intestines. Further study showed that in the smaller specimen there was preserved the *entire* alimentary canal and the other specimen had the alimentary tract approximately complete. There are no traces of branchiæ to be observed in either specimen.

The species which these forms represent is unknown and the writer has accordingly proposed for them, in another place, the name *Eumicrerpeton parvum,* new genus and species, and has regarded them as representatives of the family Branchiosauridæ. The smaller specimen has the more completely preserved canal of the two and the description given below will apply mainly to that specimen.

The nodule which contains this interesting little fossil measures two and a quarter inches by two inches and the fossil salamander occurs as nearly as possible in the center of the nodule (Fig. 4). The white kaolin which has usually replaced the bones in the Mazon Creek fossils has nearly all become eroded, only that of the right humerus remaining. The animal is of course preserved on its back.

If it were not for the fact that the œsophagus became loosened and dropped down from its place shortly after death, the alimentary canal would be in place and would immediately recall a freshly dissected specimen of a recent salamander. The anterior end of the œsophagus lies obliquely across the chest region with its tip pointing slightly downward. The length of the œsophagus proper is only about three millimeters. The entire animal measures but thirty millimeters in full length from the snout to the tip of the tail, the form of which is clearly preserved (Fig. 1).

The œsophagus, as it is preserved, lies in a semi-sigmoid curve with the convexity anterior. It enters the

cardiac portion of the stomach by a gradual constriction. The stomach is clearly preserved as a distinct sac-like organ with two lobes which correspond to the cardiac and pyloric limbs. The stomach measures about seven millimeters in length by two millimeters in its greatest diam-

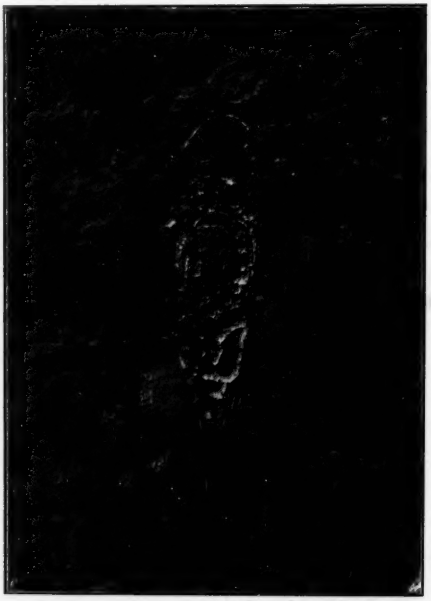

FIG. 1. An enlarged photograph of the smaller specimen of *Eumicrerpeton parvum* showing nearly the complete course of the intestine. × 2.

eter. The muscular constriction which divides the organ into pyloric and cardiac divisions occurs at a distance of four millimeters from the upper end. The pyloris is designated by a rather pronounced constriction which may be partly accidental although it recalls the pyloris of the frogs very strongly. From this constriction, which lies on the left side of the fossil, as it is preserved, the duodenal portion of the intestine makes a straight course posteriorly to near the anal region, where it takes a sharp bend and curves back to run parallel with itself for the

distance of four millimeters. In its upward course, immediately on leaving the anal region, the intestine enlarges and practically the same enlargement continues throughout the remainder of its course to the anus. At the distance of a millimeter from the anal end the rectum dilates probably an eighth of a millimeter to form the

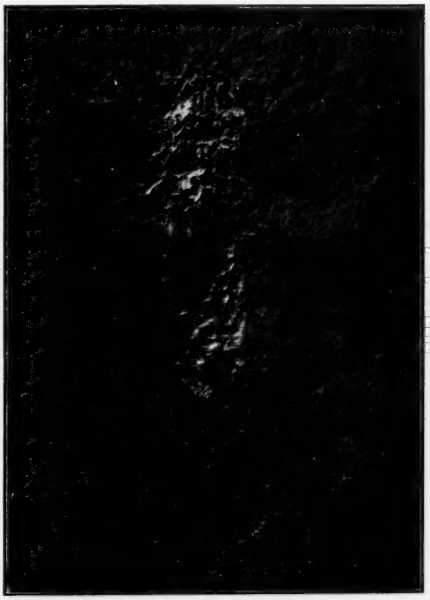

FIG. 2. An enlarged photograph of the larger specimen of *Eumicrerpeton parvum* showing portions of the impressions of the alimentary canal. ×2.

cloaca. After the intestine has continued its parallel course for the four millimeters as stated above, it turns abruptly to the right for a distance of two millimeters. It then runs posteriorly for a short distance, then bends back and under itself to again make a double sigmoid curve, when at a distance of six millimeters from the anus it assumes a straight course which it continues to the end (Fig. 3).

The anus lies at a level which is approximately that

of the lower end of the femur, which is preserved as an impression on the left side of the fossil, thus agreeing in its position with that found in the modern Caudata. Lying inside of the curve of the stomach and partly inclosed by the œsophagus is a smooth area which may

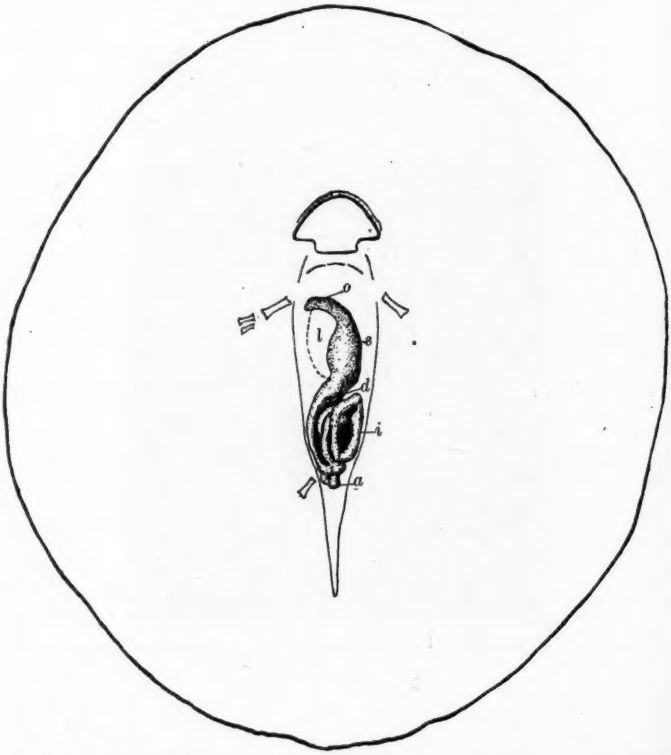

FIG. 3. A drawing of the smaller specimen of *Eumicrerpeton parvum* showing the full course and condition of the intestinal tract. ×2. *o*, œsophagus; *l*, liver; *s*, stomach; *d*, pyloris; *i*, small intestine; *a*, anus. Portions of the limb bones are also outlined as well as the anterior end of the interclavicle.

possibly represent the impression of some of the accessory digestive glands such as the liver. Occurring in this smooth area are numerous fine lines which possibly represent blood vessels; but they are so imperfectly preserved that I will not be sure.

The other and larger specimen (Fig. 2) is some ten millimeters longer than the example described above. The alimentary canal is represented not as a mold, as in the specimen described above, but by an impression from which the mold has been lost. By taking a wax impression of this specimen the form of the œsophagus, stomach and portions of the intestines, with the same form and arrangement as has been described, are beautifully shown. The œsophagus has also in this specimen been loosened and dropped down. The anus is quite prom-

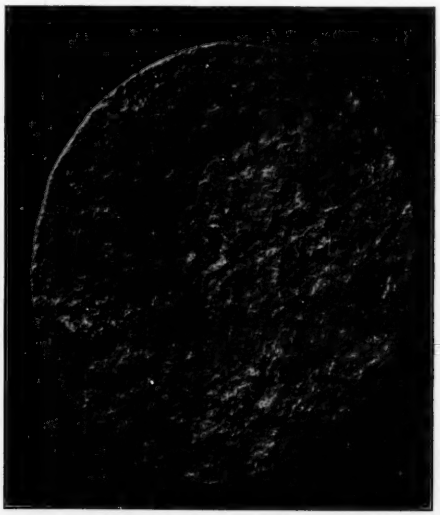

FIG. 4. The nodule containing the smaller fossil shown natural size.

inent and lies somewhat beyond the base of the tail. The tail is preserved entire in an elongate V. On its membranes are to be seen very clearly preserved the median and dorsal lateral lines which have been so completely described for *Micrerpeton caudatum*. Lying beside the anus in both specimens is a small elevation which may in both cases be accidental or it may represent either the posterior end of an oviduct or some anal gland which the branchiosaurians possessed.

The modern amphibia present many problems for consideration. Among the most interesting of these is the one which is concerned with the phylogeny of the living forms. An attempt has previously been made by the writer[1] to elucidate the problem of descent so far as the Caudata are concerned. The present contribution is a further extension of that effort and it supports the conclusions there drawn.

Representatives of several genera of the modern Caudata have been dissected in order to make a direct comparison of the fossil alimentary canal with that of the recent forms. Among the forms dissected may be mentioned *Ambystoma tigrinum, Ambystoma opacum, Diemyctylus torosus, Diemyctylus viridescens, Desmognathus fuscus* Raf., *Spelerpes bilineatus* Green, etc. In some cases representatives of several stages in the growth of the individual species have been available for study. The alimentary tract of *Desmognathus fuscus* Raf. from the vicinity of Ithaca, New York, resembles in a marked degree that of the fossil form. The nearest approach to the condition there represented is, however, found in an immature branchiate individual of some 47 millimeters in length, of *Diemyctylus torosus* Esch., from a fresh-water pond on Orcas Island in Puget Sound. The presence of this species on the island is very suggestive and its bearing on the geological age of the caudate amphibia will be given elsewhere. It is of extreme interest that the condition represented by the fossil should resemble so closely that of an immature rather than a mature form since it lends support to the recapitulation theory. Perhaps the representative species of the genera *Desmognathus, Spelerpes, Hemidactylus,* etc., are forms which have become restricted in their development and thus represent more nearly in the structure of their alimentary canal the ancestral condition, as is also the case in the immature form of the *Diemyctylus torosus* Esch.

The writer has attempted to show that the modern

[1] AMERICAN NATURALIST, XLII, No. 498, June, 1908.

Caudata are forms which have evolved by a process of degenerative evolution and he has supported his contention by a direct comparison of the skeletal anatomy of the Branchiosauria and the Caudata. So far as the skeleton is concerned the caudate organization is less high than that of the Branchiosauria. Such can not be said of the alimentary canal, for it at least has progressed in its development in many forms, although, as has been stated above, some of the more slender species are apparently restricted in their development. The fact that a young form of *Diemyctylus torosus* shows a closer approach to the fossil condition than any other is of extreme interest. It can be said with certainty that the *Diemyctylus torosus* goes through the phylogenetic stages in the development of its alimentary canal and in my opinion we have here a representative in the fossil condition of one of these phylogenetic stages. But too much importance can easily be attached to the close resemblances outlined above. It is to be remembered in this connection that the form of the alimentary canal is so highly modified by the food habits and by the form of the body of the individual animal that it will be difficult to draw safe conclusions. On the other hand, so far as we have ascertained, the form of the body of the salamanders has not changed essentially from that of their forebears, the Branchiosauria, so there is no really good reason why the form of the alimentary canal should have undergone much change.

SHORTER ARTICLES AND CORRESPONDENCE

OBSERVATIONS ON THE SPAWNING HABITS OF HYDROIDES DIANTHUS

In connection with experiments and observations on the behavior of several species of annelids, chiefly the one above named, covering a period of several years, it was my good fortune to have seen the apparently somewhat rare phenomenon of the spawning of these annelids under circumstances peculiarly favorable for observation. So far as I am aware this has not been made a matter of record, at least for this species, and some inquiry among students of the group has failed to elicit any detailed knowledge concerning the subject. It seems to be worth while to submit my notes made at the time for at least a record of fact, trusting that they may prove interesting to that extent.

The observations were made upon specimens in an aquarium in my room at the Fisheries laboratory, Woods Hole, on July 30, 1908. A large colony, or aggregate, of these annelids had been freshly obtained from near New Bedford, and had been transferred to my aquarium about two hours before the spawning took place. This was soon after noon of the date mentioned and the first appearance of the discharge took place about two o'clock. I was sitting quietly by the aquarium observing the various aspects and attitudes of the specimens, when a single individual was seen to discharge suddenly a jet of whitish matter, which seemed like a milky spume. It was so unusual as to attract immediate attention, and within a few seconds the same specimen repeated the process. Almost immediately a second specimen made a similar discharge, ejecting a cloudy mass in a jet which extended from twenty to thirty millimeters from the worm, which at the time was extended perhaps about half that distance beyond the orifice of the tube. Almost immediately another specimen exploded in similar fashion, and in less time than it requires to make the record there were dozens actively discharging clouds of eggs and sperms, until the entire mass of water (at least six gallons), was milky with the generative products. The eggs soon settled downward, indeed at the time

of ejection they were easily distinguishable, being ejected to a less distance and rapidly inclining toward the bottom. The spermatozoa, on the other hand, remained floating for an hour or more after the discharge had ceased. The operation went on for a period of some thirty or forty minutes, and then ceased almost as suddenly as it had begun. Within an hour or so the water had cleared of its milky aspect, the cells having settled to the bottom of the tank.

The phenomenon was unlike anything which I had ever seen among annelids. A single specimen would discharge at brief intervals in jets like puffs of steam from an engine, and at the height of the performance, when at least fifty specimens were thus engaged, it was a spectacle of the most striking and exciting character. If one could imagine some Lilliputian fire brigade of similar numbers all intent on discharging intermittent streams upon a miniature conflagration the impression could hardly be more engaging!

Antecedent Behavior.—It had been observed at the time of the transfer of the specimens referred to above, that there were quite a number of large specimens which did not retract fully into the tubes, as is usually the case under such an operation. This aspect was more or less persistent during the operation of handling, and if a specimen were compelled to fully retract by touching it with the finger it would soon reappear and protrude the anterior portion of the body. This protrusion was likely to continue even after they had been put quietly into the aquarium. It was this peculiarity which was engaging my attention at the time the sexual explosions began. The query arose as to whether it might not have been induced by some stimulus associated with the process of transfer and consequent exposure to extraneous conditions. Accordingly I took occasion to subject the colony to similar handling on subsequent days in order to assure myself concerning the matter. But in no case was it possible to induce a second discharge, or any simulation of the sort. It seems highly probable, therefore, that the phenomenon was perfectly normal, notwithstanding its apparently unusual character. During the several years in which I had similar colonies under observation in the same room for long periods it would seem as if *some* symptom of the sort might have been noted. In a letter from Professor J. Percy Moore I am assured that

Although I have kept large numbers of *Hydroides* literally bursting with genital products under observation, I have seen natural oviposition only twice.

Professor A. L. Treadwell has also stated that he has observed a similar operation in the egg-laying of *Dopatra*. He says further:

Whether the epidemic of egg-laying, in which when one starts the others follow, is due to a similar stimulus acting on all of them at once, or whether the first one stimulates the others, is not certain. I should consider the latter the more probable explanation. I found that to be the case in *Podarke*, where, if one started, the whole dish was apt to explode.

So far as could be ascertained under casual observation the individuals participating in the performance were about equally males and females, a further indication of the essentially normal character of the phenomenon. It would seem as if specimens of approximally similar age and condition of maturity ripen the genital products at a given time, and under the appropriate stimulus discharge them simultaneously.

The behavior will recall the somewhat similar exhibition of the pololo worm, whose swarming and coincident spawning has been described by several observers. May we not conclude that these several phenomena are but varying expressions of a spawning habit more or less common in annelids, and indeed not unknown among other of the lower invertebrates, though differing of course in various details?

It may be mentioned in conclusion that the ova discharged by the worms at the time described were promptly fertilized and developed in a perfectly normal and regular fashion.

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SYRACUSE UNIVERSITY,
January 14, 1910.

NOTES AND LITERATURE

PROTOZOA

Doflein's "Lehrbuch der Protozoenkunde."[1]—No group of animals affords a more direct approach to the problems of evolution than the Protozoa and few offer such varied data for their discussion. The organism and the individual are here reduced to lowest terms and the processes of growth, differentiation, degeneration, regeneration and reproduction in the most varied forms are found in astonishing variety and complexity. The phenomena of overcrowding, rapid destruction, parasites and parasitism, immunity, variation, speciation, isolation and perhaps even mutation, with all of their consequences on structure and reproduction, are illustrated in varying degrees of diversity and completeness. It is therefore to be expected that a thoroughgoing review of the rapidly augmented literature of protozoology by Professor Doflein will yield some new points of view or at least a new perspective in which old conclusions and hypotheses may be tested.

The biogenetic law, for example, in the opinion of the author of the "Lehrbuch" is very doubtfully applicable to the Protozoa. External factors profoundly affect the form and structure of these simple organisms. Increased alkalinity of the water changes *Amœba limax* to *A. radiosa,* as Verworn has shown. Trypanosomes vary greatly in appearance and virulence, according to the hosts in which they are cultivated, and in culture media locomotor organs are lost and nucleus and blepharoplast are shifted into new relations in the cytoplasm. Reproductive processes are profoundly modified by temperature and chemical media. The kind of food, according to Faure-Fremiet, affects the structure of *Vorticella.* The form changes, therefore, through which a protozoan runs in its life cycle are to be regarded as moulded by external influence rather than by internal factors of heredity and the production of similar structures is a phenomenon of convergence rather than a proof of relationship or descent.

This point of view determines Doflein's treatment of certain important questions. Thus the Suctoria form a class coordinate

[1] "Lehrbuch der Protozoenkunde." Eine Darstellung der Naturgeschichte der Protozoen mit besonderer Berücksichtigung der parasitischen und pathogenen Formen. Zweite Auflage der "Protozoen als Parasiten und Krankheitserreger." Von Dr. F. Doflein. Pp. x + 914. Mit 825 Abbildungen im Text. Jena, Gustav Fischer, 1909. M. 24. Geb. 26.50.

with the Ciliata since the posterior circlet of cilia formed on the bud of *Acineta* is a convergence phenomenon attendant upon the free-swimming life of this stage rather than primarily an ancestral character indicating the derivation of the Suctoria from the Ciliata.

Again the occurrence of flagellate-like stages in the life history of the *Plasmodium, Babesia* and *Leishmania* is not regarded as of phylogenetic significance but as an independently derived adaptive stage. The Hæmosporidia are therefore not transferred from the Sporozoa to the Flagellata by Doflein as Hartmann and others have argued. On the other hand, the trypanosomes are regarded as having been derived from parasites of insects such as *Herpetomonas* and *Crithidia,* whose forms they resemble in culture media.

Doflein is skeptical about the specific distinctness of the various pathogenic trypanosomes of mammals, though recognizing the necessity of distinguishing them to avoid confusion, by their hosts, occurrence and typical form in the blood of the host. They are forms merely, not fixed species, and doubtfully even incipient species. He holds as uncertain even the specific distinctions in the so-called gametes of *T. gambiense* and *T. brucei* in the tsetse fly reported by Koch. He also rejects as hypothetical the sexual cycle of *T. lewisi* in the rat louse reported by Prowazek, regarding the evidence as based on abnormal stages altogether too rare in occurrence to be typical sexual phases. However the more recent work of Minchin, Baldry and Breinl and Hindle tends to confirm the view that a sexual phase of the parasite may occur in the insect host.

The Protozoa are regarded as a group whose limits are arbitrarily defined in the interests of economy in scientific work rather than by structure. No sharp boundary line separates then on the one hand, from the Metazoa—witness the spore of *Nosema* or that of the *Actinomyxidia*—or, on the other, from the lower Metaphyta, as may be seen in the family Volvocidæ within which numerous types of colonial organization have been evolved. Not only do the Protozoa intergrade with Metazoa, the lower algæ, moulds and fungi in morphological characters, but also in physiological as well.

The author has for some years consistently maintained that the lowest branch of the Protozoa is not the Rhizopoda as stated in practically all text-books and manuals, but rather that the Mastigophora are to be regarded as lowest in the scale of organization. This is based not only upon the occurrence of flagellated forms in the gametes or other reproductive phases in the life history of

other classes, but also upon the relationships of the Mastigophora to the Bacteria. This relationship is traced by Doflein through the Spirochætes which he names also Proflagellata, to *Spirillum* and like forms. The suggestion is made that the Bacteria are the equivalents of postulated Monera of Haeckel, though they are far from resembling the forms actually described by him as Monera, and that bacteria other than *Spirillum* should be in like manner attached to other groups of protists to which they may be related. Attention is called to the wide-spread occurrence among Protists of chromidial cells, that is those seemingly without nucleus but having finely divided and distributed chromatin as seen in Bacteria, *Oscillaria, Nostoc* and *Tetramitus* and to the appearance of this same type of distribution of chromatin throughout the cell body among Protozoa at certain stages of life history, especially in gametogenesis, though also in hunger-stages and in pathological conditions. He wisely sounds a note of warning against the domination in protozoology of the morphological conception based upon the Metazoan cell, and a note of caution against the possible interpretation of minute parasites as chromidia. Ingested chromatin, as Martin has shown in the Suctoria, also offers a pitfall for the chromidia hunter.

The theory of Schaudinn and Goldschmidt of the fundamental dualism of the nuclear substance in the Protozoa, of the existence side by side in the cell of sexual chromatin as exemplified in the micronucleus of *Paramecium,* of the generative chromidia of the Foraminifera, and the nuclear membrane substance of *Acanthometra* and of somatic chromatin as seen in the macronucleus of the ciliates, he regards as only a convenient morphological schema not justified by either the comparative morphology or the physiology of the Protozoa as a whole. He inclines rather to Hertwig's view of the unity of the chromatin substance.

Dr. Doflein acknowledges the great service which the theory of Hertwig regarding the proportions of nucleus and cytoplasm has rendered to science in the stimulation of research, but looks to the future to assess its permanent value. He suggests that depression stages resulting, on the one hand, in the regulating processes of sexual reproduction or, on the other, in degeneration and natural death, are exceptional "in der freien Natur." To the reviewer the astounding fluctuations[1] in numbers which the organisms of the fresh-water plankton undergo in short periods of time of three to five weeks, rising from minimum numbers to

[1] Kofoid, C. A., 1908, "Plankton of the Illinois River," Pt. II, Constituent Organisms and their Seasonal Distribution, *Bull. Ill. State Lab. Nat. Hist.*, V. 8.

maximum of extreme proportions and falling away again with equal or greater abruptness with accompanying high death rate and appearance of sexual reproduction, especially in rotifers, seem to be of a similar nature to the cycles with intervening depression periods in laboratory cultures. These occur, moreover, constantly and with surprising regularity in nature, in both marine and fresh-water plankton among organisms of short life-cycles.

Certain points in both Schaudinn's and Hertwig's theories of sexual reproduction are combined with the earlier suggestions of Bütschli in a theory of sex which has much in common with that put forth by Geddes and Thomson. Living cells are conceived as consisting of two groups of substance, one more fluid in consistency concerned with the dynamic activities such as cell division and locomotion, the other more solid, the reserve stuff for the activities of life. In cell division these substances are not equally distributed, reserve stuff predominates in some (females) and the locomotor substance in others (males). Morphological cell constituents for these substances are expressly not postulated. An indifferent protozoan by division gives rise to equal numbers of differentiated male and female individuals, whose differentiation increases as division progresses. Fertilization takes place in consequence of the physico-chemical attraction of the two substances. The same chemical differences which condition the form-distinctions of the gametes are also the prime cause of the union in fertilization.

This theory naturally is easily applicable to the indifferent, male and female forms of Trypanosomes and to the highly differentiated sexual process and gametes of the Sporozoa generally, but requires further elucidation to make it applicable to isogamy, which is perhaps the primitive type of sexual reproduction and one seemingly widespread among Protozoa.

Dr. Doflein's book is not only a great mine of carefully and critically assembled information on Protozoa, but his facts are marshaled with reference to the great problems underlying all biological work in such a way as to stimulate further research.

CHARLES A. KOFOID.

UNIVERSITY OF CALIFORNIA.

CELEBRATING DARWIN'S GREATNESS AND DARWINISM'S WEAKNESS

IT will seem less ungracious now that the year has turned, the one-hundredth year since Darwin's birth and the fiftieth

since the "Origin of Species," to say that the many memorial meetings of the past year have left the definite impression on the scientific world of having celebrated Darwin's greatness and Darwinism's weakness. This is particularly true of the most important and conspicuous two of these meetings of which the books[1] under my eye at this moment are the permanent published record.

The eleven addresses of the "Fifty Years of Darwinism" volume are, with one exception, by American naturalists. And, with that same exception, and perhaps one other, all sound clearly the note, now more pronounced, now more restrained, of positive adverse criticism of the Darwinian factors in evolution. Each speaker first recognizes the lasting debt of science and of himself to the immortal master, and then gently or forcefully proceeds to show how the master's explanation fails to explain, and to unload and display his own precious personal baggage of "factors"; factors of environment, of mutation, of adaptation, of determinate variation, of isolation and what not.

It is, of course, greatly gratifying to us all, in these very times of loud bewailing of the insufficiency both in quantity and in quality of American output in research and natural-philosophic thought, that each of the distinguished speakers at the chief American Darwin memorial meeting had his own personal baggage of evolution contributions to unload. In a pinch we can make, by discriminating concentration, a very creditable showing for American activity in the biological "higher thought." "Fifty Years of Darwinism" certainly proves this.

The exception to the chorus of criticism and contributions to substitute for the selection theories, or, at any rate, to come to their imperatively needed aid because of some partial but fatal weakness, is embodied in the address of the one English participant in the meeting. Professor Poulton, with a glorious patriotism that surpasses that of the defender of imperialism, of an hereditary legislative body or a staggering naval budget, defends all of Darwinism against all of its critics.

For the rest, the names of Chamberlain, Coulter, Jordan, Wilson, MacDougal, Castle, Davenport, Eigenmann, Osborn and Hall show the scope and authority and interest of these addresses.

At the great English meeting there were more than twice as

[1] "Fifty Years of Darwinism," Eleven Centennial Addresses in Honor of Charles Darwin, 1909, H. Holt & Co., New York, $2.00.

"Darwin and Modern Science," Essays in Commemoration of the Centenary of the Birth of Charles Darwin and of the Fiftieth Anniversary of the Publication of "The Origin of Species," 1909, University Press, Cambridge, and G. P. Putnam's Sons, New York, $5.00.

many essayists and the book that publishes them is twice as large as the American book. Of the twenty-nine speakers eighteen were British and eleven foreign (two American, six German, one French, one Danish and one Dutch). Also the subject covered was much broader than that of species-forming, heredity and adaptation. It ranges from embryology to the genesis of double stars; from the structure of the cell to the bases of religious faith; from the movements of plants to the evolution of matter. The greatest Neo-Darwinian and one of the greatest Neo-Lamarckians were there; as were the most radical mechanicalist, the most advanced monist, the most ardent Mendelian, the founder of the mutations theory, one of the most influential of modern philosophers, and the four distinguished sons of the immortal master. It was a more representative gathering than the American one if for no other reason—though there are other reasons—than that twenty-nine men are likely to be more representative than eleven, or that six nationalities are likely to represent more than two.

But the points in common to both meetings were exactly those indicated by the title of this review. And these are the points common to almost all present-day critical discussion of evolution and its explanations. Darwin's explanations are no longer sufficient; they never were, of course, but they seemed so. But Darwin himself as man and worker, as example, as real establisher and greatest champion of the whole organic evolution conception, shines ever more brilliantly in the heavens of history.

De Vries, Weismann, Bateson, Haeckel, Lloyd Morgan, Goebel, Klebs, Sedgwick, W. B. and D. H. Scott, Loeb, Schwalbe, Arthur Thomson, Strassburger, Joseph Hooker, Thiselton-Dyer, Gadow, Francis and George Darwin, Poulton, and the nine others that represented geology, physics, philology, history, sociology, philosophy and religion, make up an imposing list of names in modern biological science. It is the list of the essayists at the Cambridge meeting. Add to it the names, already catalogued, of the participants in the American meeting, and the possessor of the two books that contain these many addresses and essays may confidently assume himself to be in possession of the latest authoritative word in evolutionary matters.

V. L. K.

STANFORD UNIVERSITY,
February, 1910.